COMPENSATORY GROWTH FOLLOWING WINTER FOOD DEPRIVATION IN HATCHERY PRODUCED COHO AND CHINOOK SALMON SMOLTS

By

Stan P. Triebenbach

RECOMMENDED:

Advisory Committee Chair

Director, Fisheries Division

APPROVED:

Dean, School of Fisheries and Ocean Sciences

Dean of the Graduate School

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Date

COMPENSATORY GROWTH FOLLOWING WINTER FOOD DEPRIVATION IN HATCHERY PRODUCED COHO AND CHINOOK SALMON SMOLTS

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By

Stan P. Triebenbach, B.A.

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Abstract

This study investigated whether coho and Chinook smolts that experienced food deprivation during the winter would increase growth rates in the spring and attain the same physiological attributes as smolts fed to satiation twice per week during the winter. The treatment groups were deprived of food for 10 and 16 weeks, centered on the winter solstice. All groups were returned to daily satiation feeding at the end of the respective food reduction periods. Treatment fish were smaller than control fish after food deprivation but had higher growth rates after feeding resumed and the 10 week fish were not significantly different in size from the control fish at the end of the study. Protein and lipid content decreased during deprivation, while moisture and ash content increased, but all groups were not different by the end of the study. Gill ATPase activity was unaffected by deprivation. Hematocrit levels declined in response to deprivation but a consistent response was not observed after feeding resumed. Coho and Chinook smolts subjected to winter food deprivation grew faster in the spring, restored body composition, and did not lose osmoregulation ability but the long-term effects on body size are unknown.

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Introduction

Each year in Alaska, hatcheries release millions of salmon fry and smolts of the genus *Oncorhynchus* to enhance commercial and recreational fisheries. In 2006, roughly one-fifth of the 123 million salmon harvested in Alaska came from hatchery released fry and smolts (White 2007). Because they can be released into the ocean shortly after emergence, making them relatively inexpensive to rear, pink (*Oncorhynchus gorbuscha*) and chum (*O. keta*) salmon constitute the majority of the releases (White 2007). Coho (*O. kisutch*) and stream-type Chinook (*O. tshawytscha*) are a much smaller portion of the annual hatchery releases because they typically require an additional year of growth in freshwater before they can be released. Due to the necessity of this extended freshwater rearing, hatcheries must invest substantial labor and finances into producing these smolts, which may experience poor marine survival. Any increases in survival and improvement in efficiency of production of coho and Chinook smolts could reduce the cost per adult produced.

To increase survival rates, hatcheries have adopted rearing strategies that attempt to mimic natural conditions to produce smolts that have growth histories and physiology similar to wild smolts. In the wild, the parr life history is characterized by a period of winter dormancy where little to no growth occurs due to low water temperatures, low food availability, and short photoperiod. This dormancy is followed by high growth rates in the spring as photoperiod becomes increasingly longer and water temperatures and food availability increase. Hatcheries can mimic this phenomenon by inducing compensatory growth in the pre-smolts with restriction of food, temperature, or photoperiod. Compensatory growth consists of elevated growth rates and rapid restoration of lost energy reserves, which allows organisms to minimize size differences with their non-restricted cohorts (Ali et al. 2003). In salmonids, compensatory growth has been demonstrated in laboratory experiments on sockeye (*O. nerka*; Bilton and Robins 1973), Chinook (*O. tshawytscha*; Hopkins and Unwin 1997), coho (*O. kisutch*; Rumble 1997), and Atlantic salmon (*Salmo salar*; Reimers et al. 1993, Nicieza and Metcalf 1997); and in wild brown trout (*S. trutta*; Johnsson and Bohlin 2005).

Historical hatchery practice promoted growing smolts as large as possible before release. While this practice produces large smolts that are more likely to survive than smaller smolts (Bilton et al 1982, Bilton 1984, Martin and Wertheimer 1989, Koenings et al. 1993, Lum 2003), it can also have the undesirable effect of producing more early-maturing males than wild populations (Larsen et al. 2004, Larsen et al. 2006), which reduces the number of harvestable adults and increases the cost per adult produced. Recent research suggests that the transition from no growth in the winter to rapid growth in the spring is associated with smolting success and survival (Beckman et al 1998, Beckman et al 1999, Beckman et al. 2000). Larsen et al. (2001a; 2001b) found that ration reduction and low temperatures during the winter had no effect on the smolting ability and condition of Chinook smolts, and it is possible that smolts may be able to tolerate further alterations of rearing conditions without detriment to their health (Larsen et al. 2006). As a result of these findings, many hatcheries have switched to a schedule of feeding to satiation only a few days per week during the winter to maintain body size and encourage rapid growth in the spring.

The purpose of this study was to determine the effects of 10 and 16 weeks of winter food deprivation on hatchery produced coho and Chinook smolts and compare the results to fish fed on a reduced-feeding strategy similar to what many hatcheries use. Induced compensatory growth in response to complete food deprivation could further elevate growth rates in the spring and thus, survival. Based on the results of food restriction or deprivation in other studies, it is believed that coho and Chinook smolts can recover from periods of food deprivation without impairment of smolting ability or alterations of body composition and body size. Increased survival would improve economic efficiency of hatcheries by decreasing the average cost per returning adult fish produced; fishermen would benefit from increased survival by the extra fish available for harvest.

Length, weight, condition factor, specific growth rates, proximate composition, hematocrit levels, and gill Na^+/K^+ ATPase activity were used as indices to measure the effects of the deprivation feeding strategies at various stages of the study. At the end of the study, the fish were dissected to determine if deprivation had an effect on the incidence of early male-maturation.

Methods

The study was conducted in the University of Alaska Fairbanks broodstock laboratory at the Douglas Island Pink and Chum (DIPAC) Macaulay Salmon Hatchery in Juneau, Alaska. In October 2005, coho and Chinook parr (brood year 2004) were obtained from hatchery production raceways and placed in 100 L tanks to begin the freshwater rearing stage. The study consisted of two rearing stages: 28 weeks in freshwater and 10 weeks in seawater. The fish were allowed to acclimate to the tanks for a couple of weeks and were fed on the same schedule until the 16 week food deprivation treatment began in late October.

Freshwater Stage

Parr were divided among twenty-four 100 L opaque, cylindrical, plastic tanks, with 150 fish per tank and four tanks per treatment. Water flow rates were controlled separately on each tank and set between 90-104 L/hour. Water was supplied from the same source as the Macaulay Salmon Hatchery production raceways, with temperatures that varied seasonally (Figure 1). The tanks were covered with opaque lids and light was supplied by a 15-watt incandescent light bulb suspended from the lid. The lights were controlled by digital timers and adjusted weekly to the local photoperiod (latitude 58° 18'N). In April 2006, 55 fish from each tank were tagged with a passive integrated transponder (PIT) in the abdominal cavity to identify the fish after transfer to the seawater tanks.

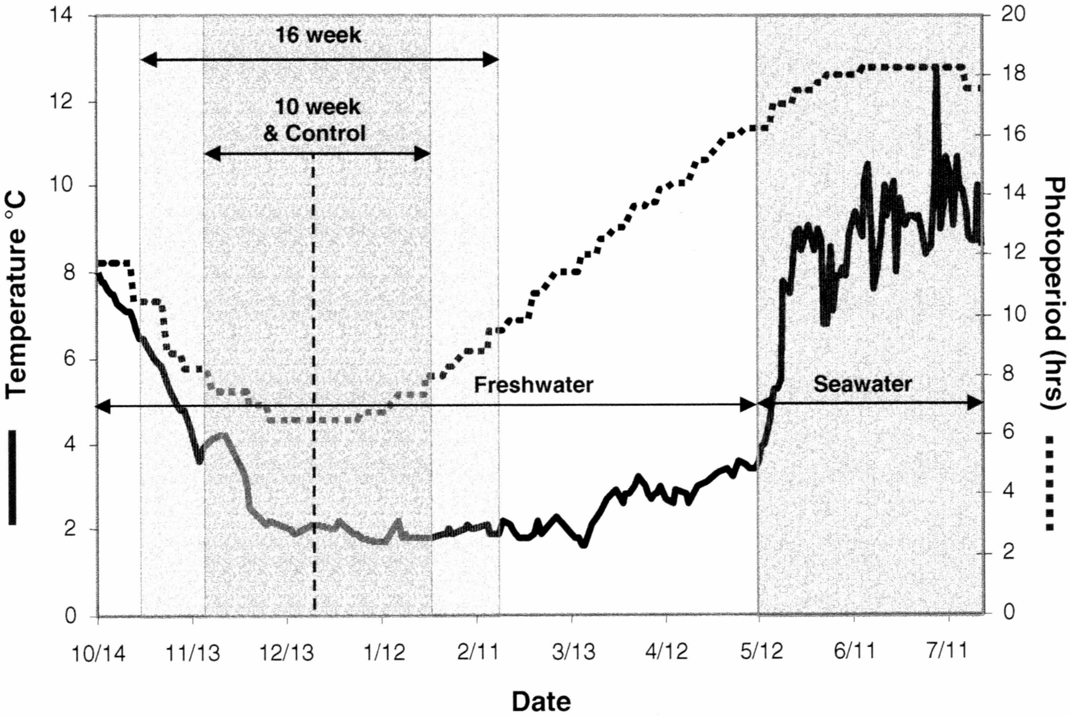

Figure 1: Water temperature (solid line) and photoperiod (dashed line) during the study of over-winter food deprivation in hatchery-reared pre-smolt coho and Chinook salmon. Shading and labeled arrows indicate dates of treatments and of freshwater and seawater culture. Treatments consisted of complete food deprivation for 10 and 16 weeks centered on the winter solstice (Dec. 21, indicated by vertical dashed line). All fish were transferred to seawater tanks in mid May. The average salinity during seawater rearing was approximately 23.

Seawater Stage

On May 13, 2006, the PIT-tagged smolts from all treatments were transferred into two, 1,700 L seawater tanks, one tank for each species. Thirty-five of the untagged fish from each treatment were reared in the 100 L tanks re-plumbed for seawater, for sacrificial samples for measuring hematocrit levels and gill Na^+/K^+ ATPase activity in June and July. All other remaining fish were measured, weighed, and euthanized. Water flow rates remained at 90-104 L/hour and photoperiod was ambient (Figure 1). Water flow in the 1,700 L tanks was set at 500 L/hour. Light was provided by the overhead room lights and adjusted daily by a digital controller. A wall of four foot tall black visquene was erected around the top of the tanks to prevent the fish from seeing human activity in the laboratory. One month prior to transfer to seawater, all fish were vaccinated by immersion against *Vibrio anguillarium* (AquaHealth, Ltd.).

Treatments

The two treatments consisted of food deprivation for 10 weeks and 16 weeks centered on the winter solstice (November 19 – January 28 and October 25 – February 18; hereafter referred to as "10 week" and "16 week"). The control group was fed to satiation two days per week from November 16 – January 28. Each treatment was replicated in four tanks, which were randomly assigned in order to decrease the effect of tank location on treatment.

All groups of fish were maintained on the Macaulay Salmon Hatchery feeding schedule before the treatments began: satiation feeding as many days per week as the fish would eat. Due to diminishing appetites as water temperatures and photoperiod decreased, feeding of all groups was gradually reduced from daily feeding to only three or four days per week at the beginning of the 16 week deprivation treatment on October 26. Once the treatment periods ended, the fish were returned to a schedule of feeding to satiation as many days per week as they would eat for the remainder of the study.

Fish were fed a commercial salmon diet (Skretting Apollo, Vancouver) between 0800 and 1600 hours. Satiation was determined by a decrease in aggressive feeding and excess food accumulating on the bottom of the tank. Satiation feeding was chosen to help reduce monopolization of food by large fish and ensure that all fish were obtaining as much food as they would eat. Prior to the start of the treatments periods, food was provided with an automatic feeder and observed daily to make sure that excess food was being provided. At the resumption of feeding, food was provided with an automatic feeder during the middle of the day and supplemented by hand-feeding in the morning and evening. During seawater rearing, food was distributed by a belt feeder during the day and supplemented by hand-feeding in the morning and evening.

Sampling

Sampling was not conducted at the beginning of the 16 week treatment due to equipment problems. On November 12, 30 fish of each species reared under the control regime were measured for fork length, weight, and condition factor. These fish were then sacrificed to measure hematocrit levels, Na^+/K^+ ATPase activity, and proximate composition. The weight measurements of fish from the Macaulay Salmon Hatchery production raceways on October 25 were not significantly different from the weight of the control fish on November 12 and 19 so it was assumed that the fish had not grown significantly and all groups were not different from each other at the beginning of the 16 week deprivation treatment. Therefore, the measurements on November 12 were used as baseline data for the study.

At the end of the 10 week deprivation period in January 2006 and approximately mid-month until May 13, 2006, 30 fish per tank were randomly selected to measure length, weight, condition factor, and specific growth rates. Ten of those fish were randomly selected to be sacrificed for examination of hematocrit levels, gill Na^+/K^+ ATPase activity, and proximate composition. From May 13, 2006 – July 22, 2006, length and weight measurements were collected from all PIT-tagged fish approximately every two weeks. Monthly samples for hematocrit and gill Na^+/K^+ ATPase activity were collected during seawater rearing from 10 fish per treatment in the 100 L tanks.

Food was withheld for 24 hours before each sampling session to ensure that any food was eliminated from the digestive system so that observed changes in weight were due to somatic growth only. Fish were anesthetized in MS-222 (tricaine methanesulfonate, 100-mg/L water) buffered with sodium bicarbonate to pH 7. Sacrificed fish were euthanized with MS-222 (200-mg/L).

At each sampling session, fork length was measured to the nearest 0.1 cm, weight to the nearest 0.1 g, and Fulton's condition factor (K) was calculated with the following formula:

$$K = 100 \cdot \text{weight (g)}/\text{length (cm)}^3$$

Values for length, weight, and condition factor were obtained from 30 fish per tank from November 12 to March 19, from PIT-tagged and untagged sacrificed fish from April 8 until the end of the study. Values displayed in the figures are the mean values for the treatments.

Specific growth rates (G) for both length and weight were calculated with Ricker's (1975) formula:

$$G = 100 \cdot (\log_e W_2 - \log_e W_1)/(d_2 - d_1)$$

where W_2 is the mean weight (g) or length (cm) on day 2, W_1 is the mean weight or length on day 1, and (d_2-d_1) is the number of days between measurements. The mean values for length and weight of the replicate tanks were used in the growth rate calculations during freshwater rearing. After the fish were transferred to seawater, individual growth rates from PIT-tagged fish were calculated and used in the variance analysis.

Blood for determining hematocrit levels was obtained from the severed caudal artery and collected in heparinized capillary tubes. For the November, January, and February sampling sessions, hematocrit samples were centrifuged at 5,000 rpm's for five minutes. The length of the compacted red blood cells was measured with a caliper to the nearest 1mm, divided by the total length of the blood sample in the tube, and expressed as a percent of the total blood volume. From March – July, hematocrit samples were determined using a different centrifuge. Samples were centrifuged at 11,500 rpm's for five minutes. The percent hematocrit of the sample was measured with the built-in scale on the centrifuge rotor. The hematocrit levels within each month are comparable to each other because the same equipment and procedures were used for all samples. However, hematocrit levels should not be compared between months because of the use of different centrifuges.

Gill filaments for Na^+/K^+ ATPase (enzyme number 3.6.3.9; IUBMB 1992) were collected from the first gill arch on the right side of the fish, preserved in 100 μL of SEI buffer (250 mM sucrose, 10 mM EDTA, 50 mM imidazole, pH 7.3), and stored in 500 μL microcentrifuge tubes at −80° C until analysis. The analysis was conducted according to McCormick (1993) and activity results were expressed as μmoles ADP·mg protein^{-1}·hour^{-1}. Two samples per tank were analyzed, for a total of eight samples per treatment per month. When possible, these samples came from the same fish that were selected for proximate analysis.

After gill tissue and blood were removed from the sacrificed fish, the carcasses were frozen at −80° C and saved for proximate composition analysis. Two fish from each tank were randomly selected for analysis from these preserved fish. Whole-body lipid, protein, moisture, and ash contents were measured at the beginning of the study, at the end of each treatment, at the end of freshwater rearing, and at the end of the study on July 22. Whole-body lipid content was determined gravimetrically after 24 hours of extraction in a Soxhlet apparatus, with petroleum ether as the solvent. Moisture and ash content was determined with a thermogravimetric analyzer (model TGA-601, LECO Corporation). Protein content was determined by measuring the amount of nitrogen in the sample with a protein/nitrogen determinator (model FP-528, LECO Corporation), which was automatically converted to percent protein by the machine software.

At the conclusion of the study, all remaining fish were dissected to determine the state of maturation. Maturation was determined by the presence of enlarged testes that dominated the space in the abdominal cavity, in comparison to females and immature males with gonads that were not easily visible.

Statistical Analysis

The statistical model used to analyze main effects for the majority of the study was a nested ANOVA:

$$Y_{ijk} = \mu_{ij} + F_i + T(F)_{ij} + \varepsilon_{ijk}$$

where Y_{ijk} is the length, weight, condition factor, specific growth rates in seawater, whole-body lipid, protein, moisture, ash, hematocrit, or gill Na^+/K^+ ATPase activity of the ith treatment in the jth tank of the kth fish. μ is a common constant, F_{ij} is the fixed effect due to treatment, T is the random effect due to tank nested within treatment, and ε_{ijk} is the random error term. A one-factor ANOVA was used to look for differences in specific growth rates between treatments during freshwater rearing, and hematocrit levels for June and July because the measurements came from one tank of fish for each treatment. Analysis was conducted with the General Linear Model function in SPSS version 15 (SPSS, Inc., Chicago, Illinois). A significance level of $\alpha = 0.05$ was used for all tests. Tukey's HSD post-hoc test was used to confirm the results of the F-test and determine which groups were different.

The Shapiro-Wilk test of normality was used to determine if the response variable and residuals were normally distributed. If the response or residuals were not normally distributed, a power, square root, or $\log_e$ transformation was performed to obtain normality. Whole-body lipid values were transformed with the formula (Sahai and Ageel 2000):

$$P' = \arcsin[\text{square root}(p)]$$

where p is the proportion of lipid in the sample. All data displayed in the figures are untransformed.

Residual plots were used to identify outliers and verify normality and homogeneity of variance. Data over 3 standard deviations from the mean were investigated with a Bonferroni simultaneous t-test at a significance level of $\alpha = 0.05$ to determine if they were outliers.

Results

Coho

Length and Weight

At the end of the 10 week and 16 week deprivation periods on January 28 and February 18, respectively, both groups of treatment fish were significantly shorter and weighed less than control fish ($F > 7.912$, $p < 0.01$ and $F > 17.851$, $p < 0.001$; Appendix 1 and 2; Table 1 and 2). The 10 week treatment fish were significantly smaller in length from January 28 – May 27 and weight from January 28 – June 10 (length: $F > 7.912$, $p < 0.01$ and $F > 17.851$, $p = 0.000$). The 16 week fish were shorter than the control from January 28 through the end of the study ($F > 4.681$, $p < 0.04$). At the beginning of the 10 week deprivation treatment on November 19, the 16 week treatment fish had not been fed for three weeks and were already significantly smaller in weight than the control fish ($F = 11.245$, $df = 2$, $p = 0.004$). This size difference persisted until the end of the study on July 22. Tank effect on length was significant on January 28 and April 8 – June 22 ($F > 2.089$, $p < 0.029$) and on weight from January 28 – May 13 ($F > 1.948$, $p < 0.045$).

Table 1: Mean fork length (cm; SE) of juvenile coho salmon deprived of food for 16 and 10 weeks and a control fed to satiation twice per week. An "x" indicates a significant difference (p<0.05) from the control at a given date.

	Treatment				
Date	16 week		10 week		Control
11/12/05					8.56 (0.12)
11/19/05	8.37 (0.05)		8.48 (0.05)		8.55 (0.04)
1/28/06	8.31 (0.05)	x	8.41 (0.04)	x	8.75 (0.05)
2/18/06	8.23 (0.05)	x	8.52 (0.05)	x	8.80 (0.05)
3/19/06	8.44 (0.05)	x	8.70 (0.06)	x	9.04 (0.04)
4/8/06	8.76 (0.03)	x	9.04 (0.03)	x	9.30 (0.03)
5/13/06	9.21 (0.03)	x	9.48 (0.03)	x	9.72 (0.03)
5/27/06	9.78 (0.04)	x	9.98 (0.04)		10.19 (0.04)
6/10/06	10.43 (0.04)	x	10.65 (0.04)		10.78 (0.04)
6/22/06	11.11 (0.04)	x	11.27 (0.05)		11.41 (0.04)
7/8/06	12.13 (0.05)	x	12.29 (0.05)		12.47 (0.05)
7/22/06	12.92 (0.06)	x	13.06 (0.07)		13.25 (0.06)

Table 2: Mean weight (g; SE) of juvenile coho salmon deprived of food for 16 and 10 weeks and a control fed to satiation twice per week. The weight value on 10/25 is from the Macaulay Salmon Hatchery production records. An "x" indicates a significant difference (p<0.05) from the control at a given date.

	Treatment				
Date	16 week		10 week		Control
10/25/05					6.81
11/12/05					6.66 (0.26)
11/19/05	6.05 (0.10)	x	6.96 (0.13)		6.91 (0.11)
1/28/06	5.53 (0.11)	x	5.88 (0.10)	x	7.12 (0.12)
2/18/06	5.13 (0.10)	x	6.44 (0.11)	x	7.41 (0.13)
3/19/06	6.07 (0.11)	x	7.02 (0.13)	x	8.13 (0.13)
4/8/06	6.69 (0.08)	x	7.79 (0.09)	x	8.62 (0.09)
5/13/06	8.00 (0.09)	x	8.90 (0.10)	x	9.71 (0.10)
5/27/06	9.18 (0.12)	x	9.81 (0.12)	x	10.55 (0.13)
6/10/06	10.95 (0.14)	x	11.81 (0.15)		12.25 (0.15)
6/22/06	13.84 (0.18)	x	14.63 (0.18)		15.26 (0.19)
7/8/06	18.60 (0.25)	x	19.39 (0.25)		20.19 (0.26)
7/22/06	23.48 (0.33)	x	24.12 (0.32)		25.24 (0.35)

On January 11, 29 fish died in one of the coho 10 week replicate tanks, presumably due to asphyxiation caused by a partial blockage of the water inflow pipe. The mean length and weight of fish from this tank was not different from the other three replicate tanks for the remainder of the study, indicating that this event did not affect growth. However, hematocrit levels for this tank were elevated for three months after this event and were removed from the variance analysis from January through March.

Specific Growth Rates

Length specific growth rate (LSGR) of both treatment groups decreased during the deprivation periods, but, after feeding resumed, they were significantly higher than those of the control after transfer to seawater in May (Figure 2). LSGR of both treatment groups from May 27 – June 10 was significantly higher than the control ($F = 18.129$, $p = 0.001$; Appendix 3). Additionally, LSGR of the 16 week fish was significantly higher than the control from May 13 – May 27 ($F = 13.484$, $df = 2$, $p = 0.002$) and June 10 – June 22 ($F = 9.571$, $df = 2$, $p = 0.006$). LSGR of the two treatments and the control were not different from June 22 – July 22. Tank effect on length growth rates was only significant from May 13 – June 10 ($F > 1.910$, $p < 0.049$).

Weight specific growth rate (WSGR) for both treatment groups declined during deprivation and was significantly different from the control from November 19 - January 28 ($F = 19.107$, $df = 2$, $p = 0.002$; Appendix 4; Figure 3). After feeding resumed, WSGR of treatment fish tended to be higher than the control. The 16 week fish had significantly higher WSGR from April through July 8 ($F > 4.69$, $p < 0.04$) and the 10 week fish had a significantly higher WSGR from May 13 – June 10 ($F > 14.874$, $p < 0.001$). Tank effect on WSGR was significant from May 13 – May 27 for both treatments ($F = 21.493$, $df = 9$, $p = 0.000$).

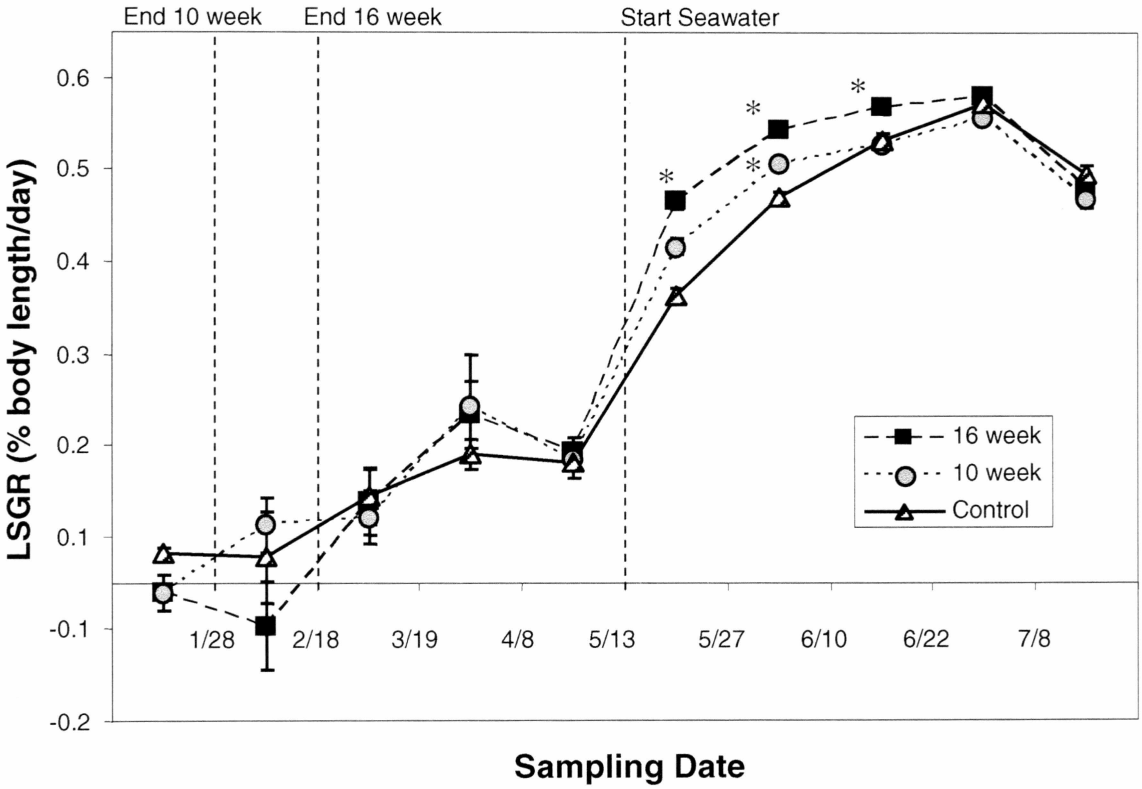

Figure 2: Mean length specific growth rate (LSGR= $100\bullet(\log_e L_2 - \log_e L_1)\bullet(d_2 - d_1)^{-1}$; ±SE) of juvenile coho salmon deprived of food for 10 and 16 weeks and a control fed to satiation twice per week. Growth rates were calculated from the tank mean until 5/13 and from the individually tagged fish after 5/13. An asterisk (*) near a marker indicates a significant difference ($p<0.05$) from the control on that date.

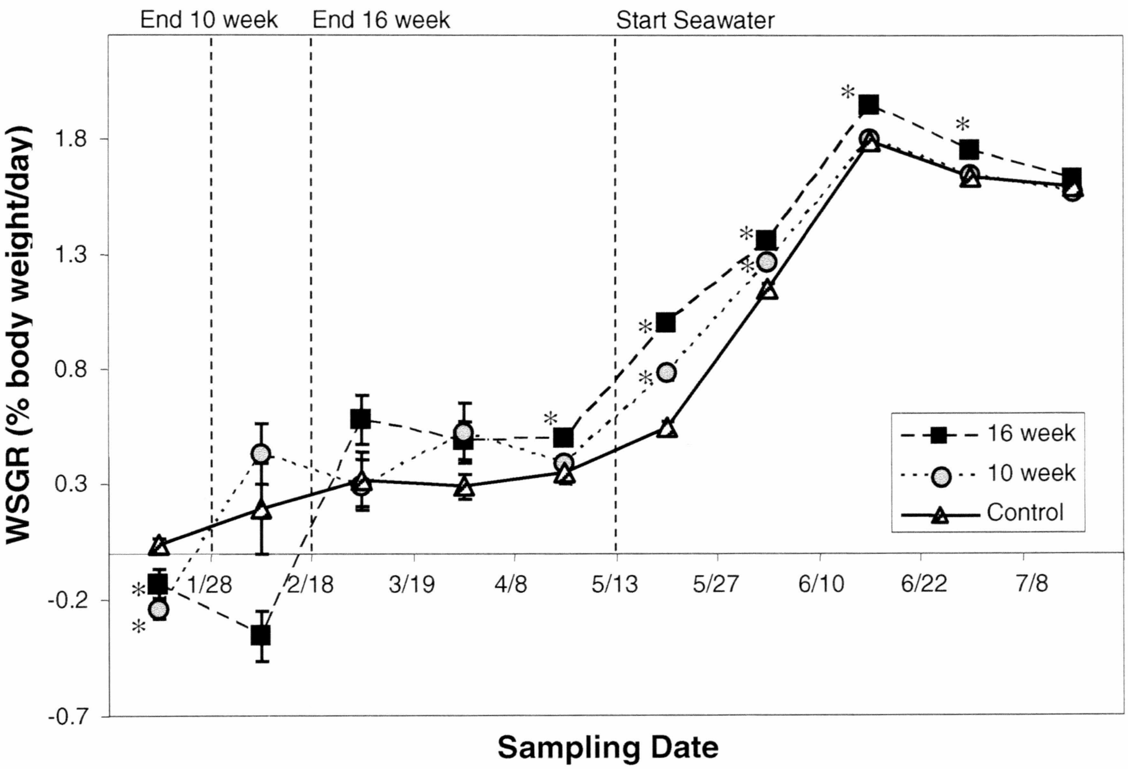

Figure 3: Mean weight specific growth rate (WSGR = $100 \cdot (\log_e W_2 - \log_e W_1) \cdot (d_2 - d_1)^{-1}$; ±SE) of juvenile coho salmon deprived of food for 10 and 16 weeks and a control fed to satiation twice per week. Growth rates were calculated from the mean weight of the replicate tanks until 5/13 and from the individually tagged fish after 5/13. An asterisk (*) near a marker indicates a significant difference ($p<0.05$) from the control on that date.

Condition Factor

During the treatment periods, both treatment groups experienced a decline in condition factor and were significantly lower than the control by the end of the respective treatment period ($F > 47.246$ $p = 0.000$; Appendix 5; Figure 4). Condition of 10 week fish remained lower than the control until May 13 and was not different from the control from May 27 – July 22. The 16 week fish had significantly lower condition from November 19 – June 22 ($F > 4.567$, $p < 0.042$) but were not significantly different from the control on July 8 and 22 (F < 1.676, p > 0.241). Tank effect on condition was significant from January – May 13 for both treatments (F > 2.675, p < 0.005).

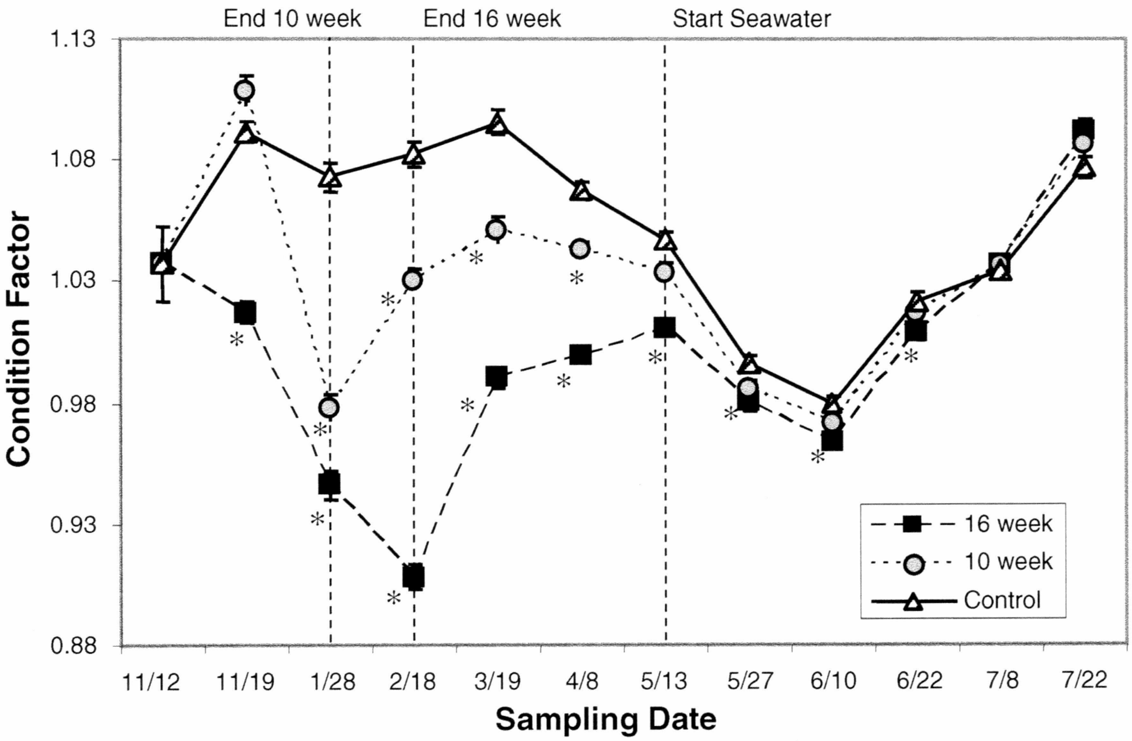

Figure 4: Mean condition factor ($K = 100 * \text{weight}/\text{length}^3$; ±SE) of juvenile coho salmon deprived of food for 10 and 16 weeks and a control fed to satiation twice per week. Means were calculated from 30 fish/tank from 11/12 to 3/19, from tagged and untagged fish from 4/8 to 5/13, and from tagged fish after 5/13. An asterisk (*) near a marker indicates a significant difference (p<0.05) from the control on that date.

Hematocrit

Hematocrit levels decreased in response to the food deprivation treatments, but the difference between treatment and the control was only detected as significant on a few sampling sessions (Figure 5). The 16 week hematocrit levels were only detectably lower than the control in January and March (F = 4.710, p = 0.045 and F = 8.037, p = 0.015, respectively). The hematocrit levels of the 10 week fish were detectably lower in March, June, and July (F > 7.284, p < 0.015; Appendix 6).The inconsistent detection of a significant difference in the mean values is in all likelihood a result of the relatively small number of samples and the distribution of the data due to differences in the mean values of the replicate tanks. Tank effect was significant on all sampling dates except in June and July because samples were taken from one tank per treatment.

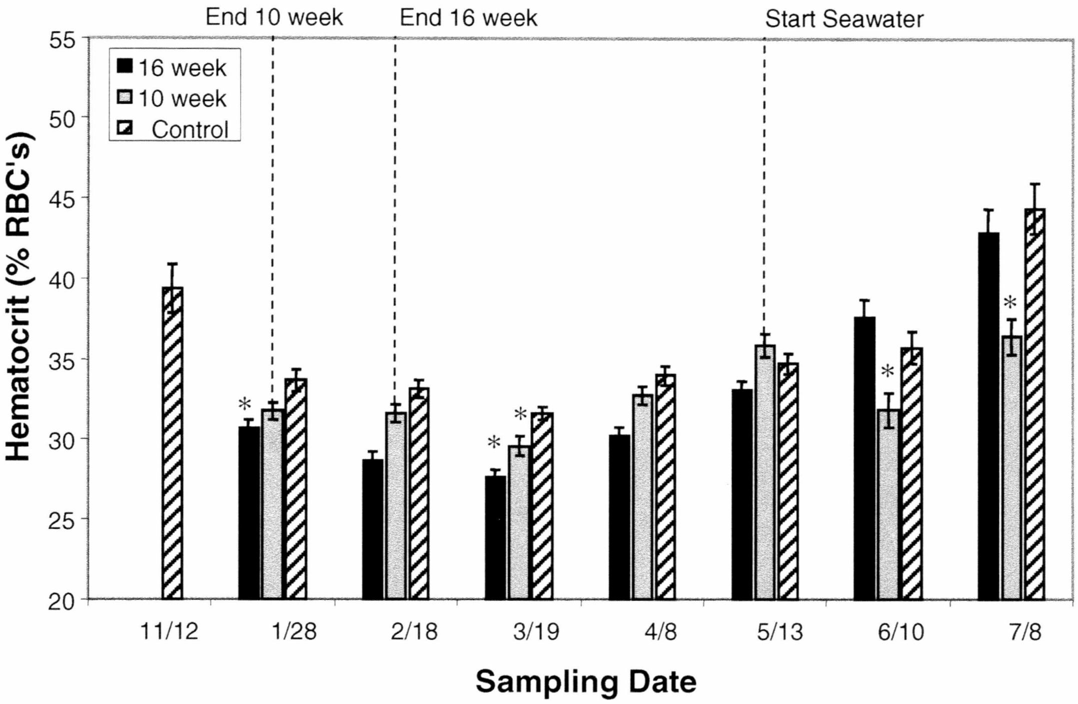

Figure 5: Mean hematocrit levels (% red blood cells; ±SE) of juvenile coho salmon deprived of food for 10 and 16 weeks and a control fed to satiation twice per week. Means were calculated from 10 fish per tank. An asterisk (*) above a column indicates a significant difference ($p<0.05$) from the control on that date.

Gill Na^+/K^+ ATPase

A decrease in gill Na^+/K^+ ATPase (hereafter referred to as ATPase) activity due to deprivation was evident for both treatment groups on March 19 ($F = 14.129$, $df = 2$, $p = 0.001$; Appendix 7) but was not significant at any other time during the study for either treatment (Figure 6). Tank effect was not significant at any time.

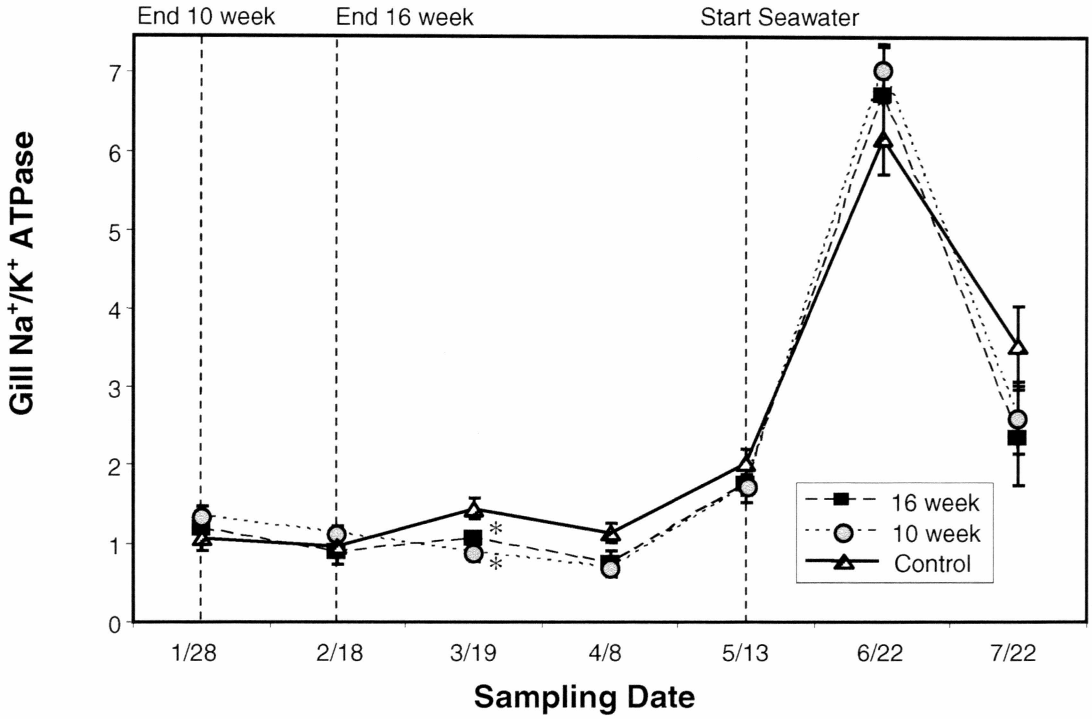

Figure 6: Mean gill Na^+/K^+ ATPase activity (μmoles ADP•mg protein^{-1}•hour^{-1}; ±SE) of juvenile coho salmon deprived of food for 10 and 16 weeks and a control fed to satiation twice per week. Means activity levels were calculated from 8 fish per treatment. An asterisk (*) above a column indicates a significant difference ($p<0.05$) from the control on that date.

Proximate Composition

Whole-body lipid and protein content of both treatment groups decreased during the deprivation periods. Although lipid content decreased, the difference from the control was not significant ($F < 4.377$, $p > 0.057$; Appendix 8; Figure 7) and lipid levels for both treatment groups were not different from the control on May 13 and July 22 ($F = 0.069$, $df = 2$, $p = 0.934$ and $F = 0.029$, $df = 2$, $p = 0.972$). Protein content in the 10 week fish decreased but was not significantly lower than the control at the end of the deprivation period and was not different from the control for the remainder of the end of the study (Appendix 9; Figure 8). The 16 week fish had significantly lower protein content at the end of the deprivation period ($F = 22.287$, $df = 2$, $p = 0.003$) and also on

May 13 ($F = 5.991$, $df = 2$, $p = 0.022$) but was not different from the control on July 22 ($F = 0.719$, $df = 2$, $p = 0.513$).

The moisture and ash content of both treatment groups increased during food deprivation, although the moisture content of the 10 week fish was not detectably higher. By May 13 the levels of moisture and ash of both treatment groups were not significantly different from the control ($F < 1.805$, $p > 0.219$; Appendix 10 and 11; Figure 9 and 10).

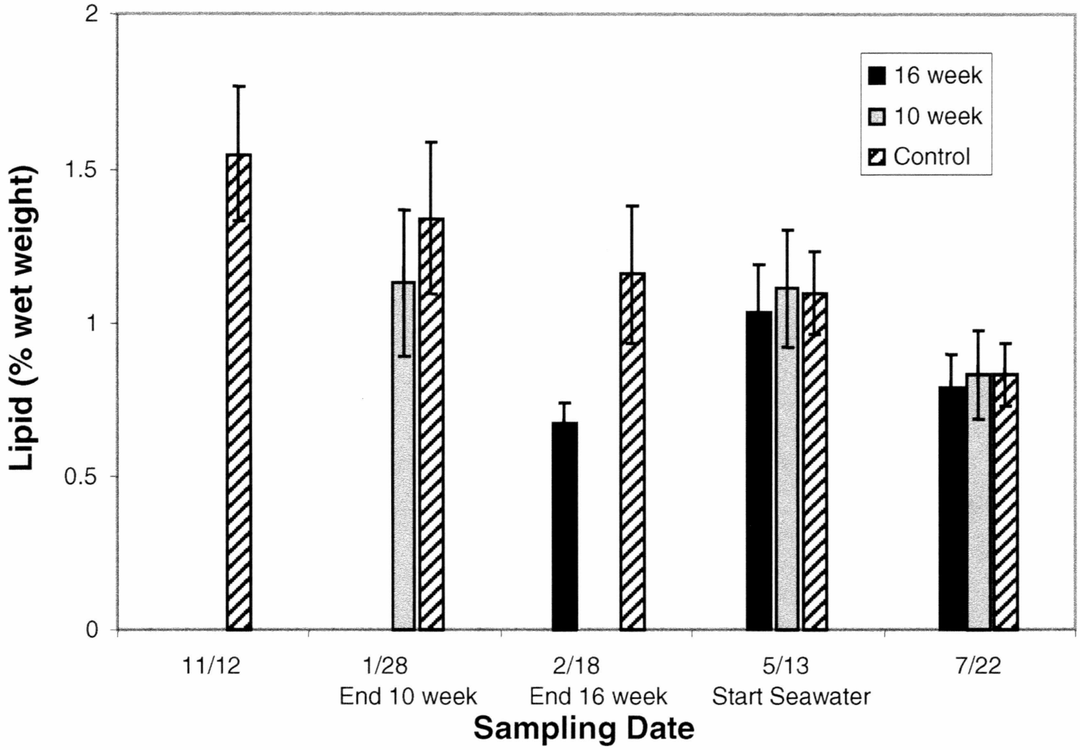

Figure 7: Mean whole-body lipid content (±SE) of juvenile coho salmon deprived of food for 10 and 16 weeks and a control fed to satiation twice per week. Means were calculated from 8 fish per treatment. Food deprivation did not have a significant effect on whole-body lipid content at any of the sampled time periods.

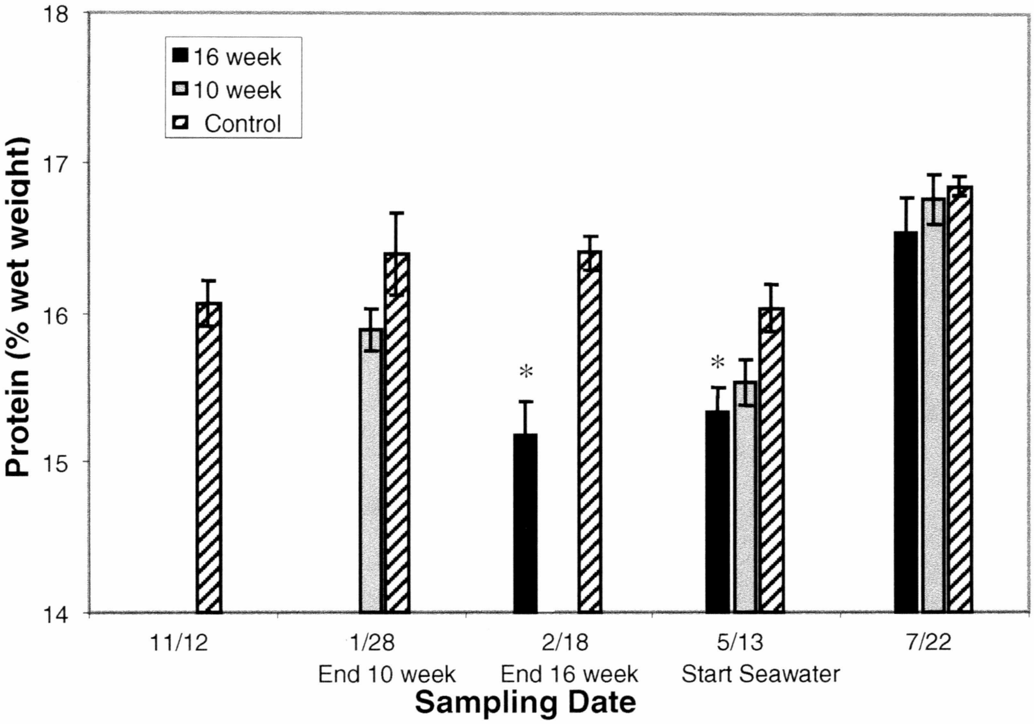

Figure 8: Mean protein content (±SE) of juvenile coho salmon deprived of food for 10 and 16 weeks and a control fed to satiation twice per week. Means were calculated from 8 fish per treatment. An asterisk (*) above a column indicates a significant difference ($p<0.05$) from the control on that date.

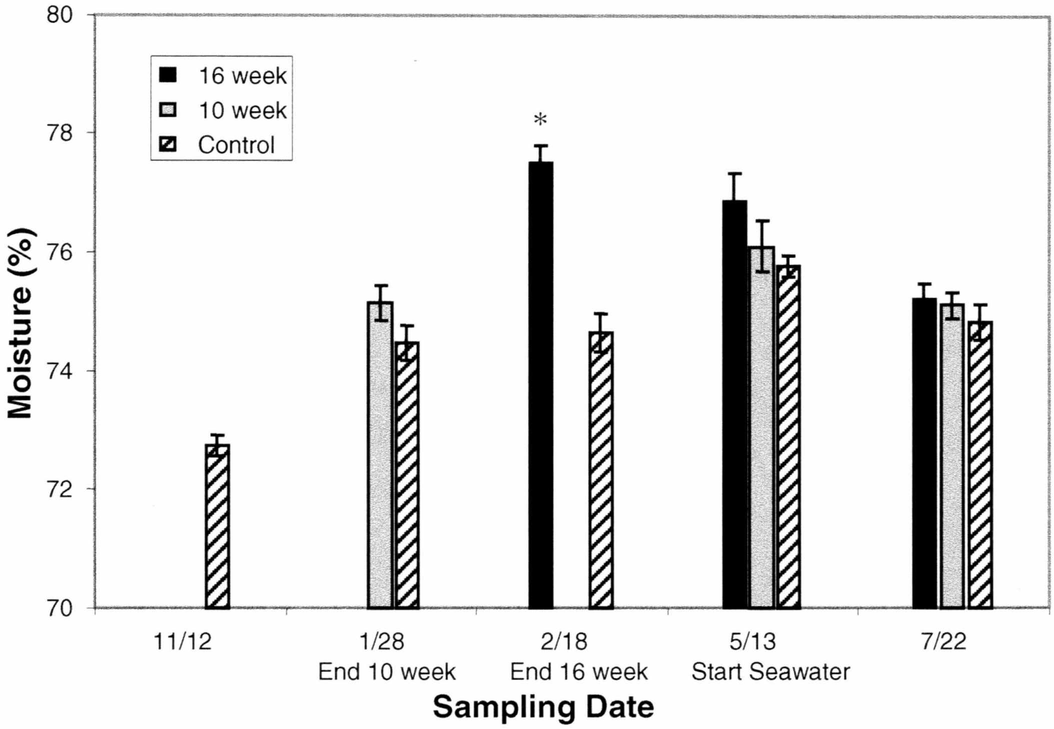

Figure 9: Mean moisture content (±SE) of juvenile coho salmon deprived of food for 10 and 16 weeks and a control fed to satiation twice per week. Means were calculated from 8 fish per treatment. An asterisk (*) above a column indicates a significant difference ($p<0.05$) from the control on that date.

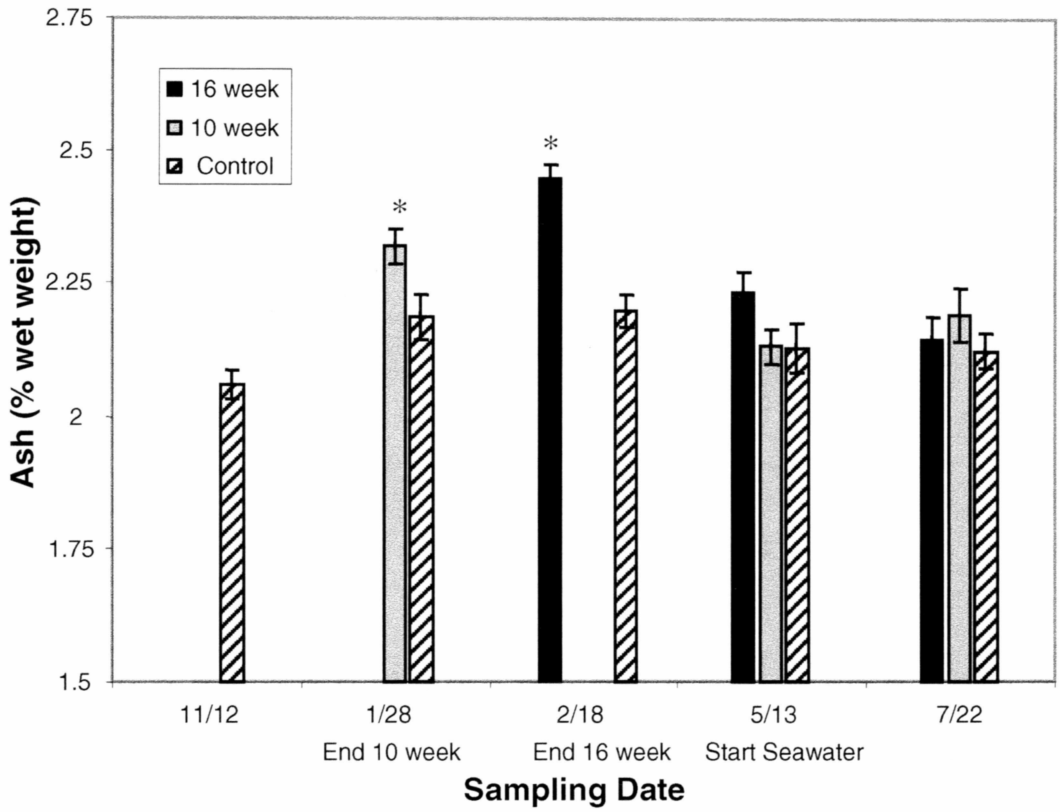

Figure 10: Mean ash content (±SE) of juvenile coho salmon deprived of food for 10 and 16 weeks and a control fed to satiation twice per week. Means were calculated from 8 fish per treatment. An asterisk (*) above a column indicates a significant difference ($p<0.05$) from the control on that date.

Male Maturation

All coho dissected for examination of maturation at the end of the study were immature; no early-maturing males were observed.

Chinook

Length and Weight

The response to deprivation by Chinook was similar to that of coho, with some minor differences. The 10 week fish were the same length as the control after deprivation but were smaller from March 19 – May 27 and they weighed less on January 28 and March 19 – May 13 ($F > 22.386$, $df = 2$, $p = 0.000$ and $F > 29.414$, $df = 2$, $p = 0.000$, respectively; Appendix 12 and 13; Tables 3 and 4). The 16 week fish were significantly smaller in length throughout the study except for November 19. On November 19, the 16 week fish weighed significantly less than the control after only three weeks of deprivation ($F = 16.617$, $df = 2$, $p = 0.001$) and this weight difference persisted until the end of the study ($F > 4.546$, $p < 0.04$). Tank effect on length was not significant on any of the sampling dates and was only weakly present in weight on May 13 ($F = 1.895$, $df = 9$, $p = 0.049$).

Table 3: Mean fork length (cm; SE) of juvenile Chinook salmon deprived of food for 16 and 10 weeks and a control fed to satiation twice per week. An "x" indicates a significant difference (p<0.05) from the control at a given date.

	Treatment				
Date	16 week		10 week		Control
11/12/05					9.49 (0.09)
11/19/05	9.29 (0.05)		9.47 (0.05)		9.41 (0.05)
1/28/06	9.10 (0.05)	x	9.40 (0.04)		9.54 (0.06)
2/18/06	9.07 (0.04)	x	9.41 (0.05)		9.46 (0.05)
3/19/06	9.21 (0.04)	x	9.48 (0.05)	x	9.65 (0.04)
4/8/06	9.43 (0.03)	x	9.63 (0.03)	x	9.78 (0.03)
5/13/06	9.68 (0.03)	x	9.92 (0.03)	x	10.10 (0.03)
5/27/06	10.00 (0.04)	x	10.22 (0.04)	x	10.40 (0.04)
6/10/06	10.82 (0.04)	x	11.02 (0.04)	x	11.16 (0.04)
6/22/06	11.43 (0.10)	x	11.76 (0.09)		12.02 (0.09)
7/8/06	12.53 (0.11)	x	12.85 (0.10)		13.08 (0.09)
7/22/06	13.58 (0.11)	x	13.95 (0.11)		14.12 (0.09)

Table 4: Mean weight (g; SE) of juvenile Chinook salmon deprived of food for 16 and 10 weeks and a control fed to satiation twice per week. The weight value on 10/25 is from the Macaulay Salmon Hatchery production records. An "x" indicates a significant difference (p<0.05) from the control at a given date.

	Treatment				
Date	16 week		10 week		Control
10/25/05					10.25
11/12/05					9.50 (0.34)
11/19/05	9.05 (0.16)	x	10.04 (0.17)		10.09 (0.17)
1/28/06	7.88 (0.15)	x	9.09 (0.16)	x	10.28 (0.19)
2/18/06	7.64 (0.14)	x	9.49 (0.17)		9.96 (0.18)
3/19/06	8.52 (0.14)	x	9.93 (0.17)	x	10.77 (0.19)
4/8/06	9.12 (0.11)	x	10.33 (0.13)	x	11.14 (0.13)
5/13/06	10.25 (0.11)	x	11.37 (0.13)	x	12.14 (0.13)
5/27/06	11.94 (0.17)	x	12.87 (0.18)	x	13.63 (0.19)
6/10/06	14.48 (0.21)	x	15.52 (0.22)	x	16.23 (0.22)
6/22/06	17.70 (0.50)	x	18.95 (0.50)		20.09 (0.46)
7/8/06	23.86 (0.67)	x	25.61 (0.69)		26.83 (0.62)
7/22/06	32.82 (0.83)	x	35.11 (0.93)		36.50 (0.80)

Specific Growth Rates

Length specific growth rate (LSGR) in the 16 week fish was lower than the control from November 19 – January 28 but LSGR of the 10 week fish was not significantly different over that time period ($F = 8.137$, $p = 0.01$, Tukey's HSD: $p = 0.008$ and 0.092 respectively; Figure 11). The 16 week treatment fish had a higher LSGR than the control from May 27 – June 10 and June 22 – July 8 ($F = 14.873$, $p = 0.001$ and $F = 4.517$, $p = 0.033$; Appendix 14). Tank effect was significant from May 13 – May 27 and July 8 – July 22 ($F = 3.444$, $p = 0.000$ and $F = 2.045$, $p = 0.037$).

Weight specific growth rate (WSGR) for both treatment groups decreased during food deprivation but were higher than the control after feeding resumed. WSGR of 16 week fish was significantly higher from February 18 – March 19 and May 13 – June 10 ($F > 6.601$, $p < 0.017$; Appendix 15; Figure 12). WSGR of 10 week fish was higher than the control after feeding resumed although not detectably higher. Tank effect on WSGR was significant from May 13 – May 27 for both treatments ($F = 3.803$, $p = 0.000$).

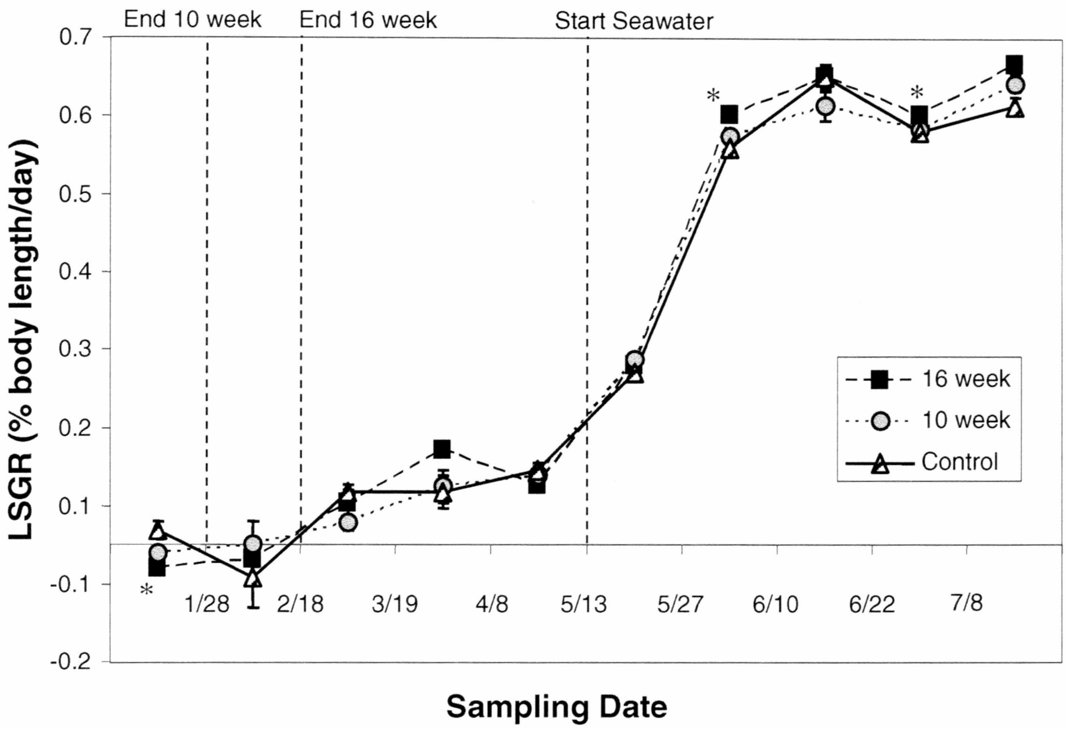

Figure 11: Mean length specific growth rate ($LSGR = 100 \cdot (\log_e L_2 - \log_e L_1) \cdot (d_2 - d_1)^{-1}$; $\pm$SE) of juvenile Chinook salmon deprived of food for 10 and 16 weeks and a control fed to satiation twice per week. Growth rates were calculated from the tank mean until 5/13 and from the individually tagged fish after 5/13. An asterisk (*) near a marker indicates a significant difference ($p<0.05$) between the 16 week fish and the control on that date. Length specific growth rates of 10 week fish were not significantly different from the control at any time.

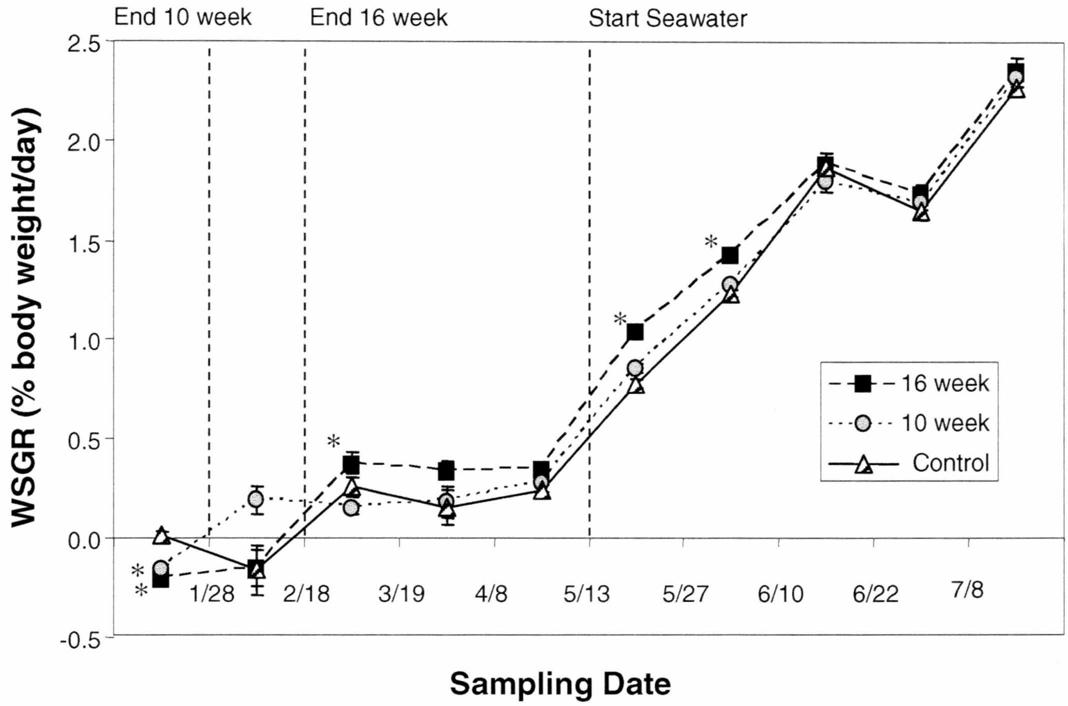

Figure 12: Mean weight specific growth rate (WSGR = $100 \cdot (\log_e W_2 - \log_e W_1) \cdot (d_2 - d_1)^{-1}$; ±SE) of juvenile Chinook salmon deprived of food for 10 and 16 weeks and a control fed to satiation twice per week. Growth rates were calculated from the mean weight of the replicate tanks until 5/13 and from the individually tagged fish after 5/13. An asterisk (*) near a marker indicates a significant difference ($p<0.05$) from the control on that date.

Condition Factor

Condition factor of both treatment groups was lower than the control after the respective food deprivation (Figure 13). The condition of 10 week fish was lower than the control on January 28 and April 8 ($F = 113.40$, $df = 2$, $p = 0.000$ and $F = 56.363$, $df = 2$, $p = 0.000$) but was not different from the control on any of the other sampling dates (Appendix 16). The 16 week fish had a significantly lower condition factor than the control from November 19 – May 27 ($F > 10.062$, $p < 0.005$) but was not different from June 10 – July 22 ($F < 1.705$, $p > 0.235$). Tank effect on condition was significant in November and March – May 13 ($F > 2.023$, $p < 0.036$).

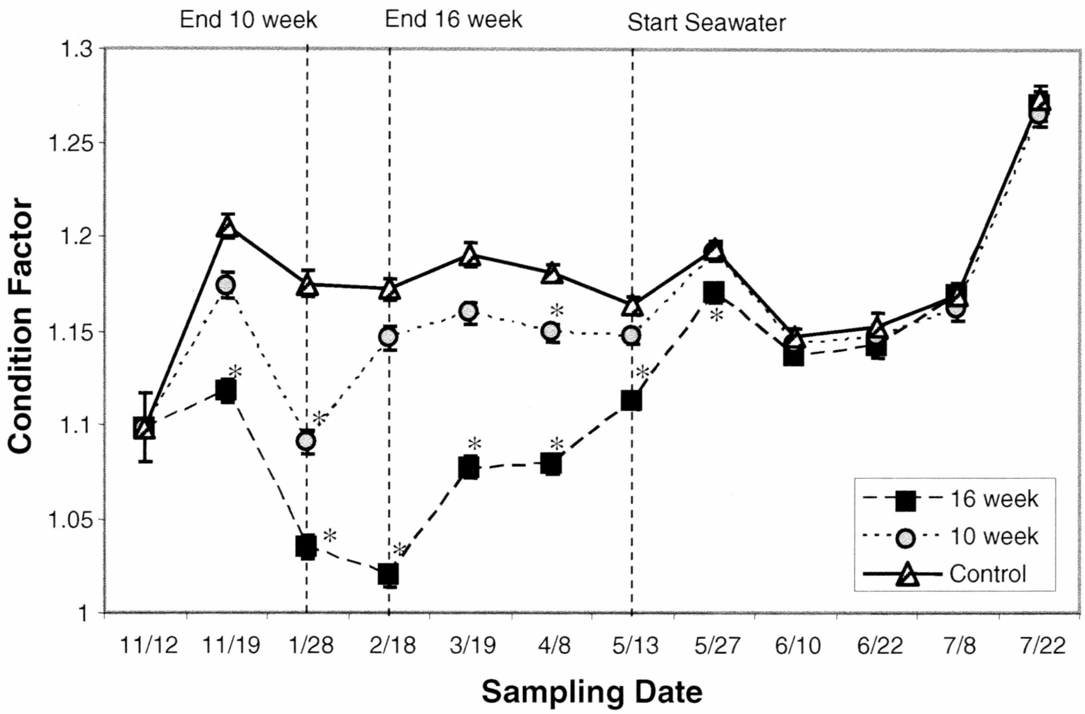

Figure 13: Mean condition factor (K = 100 * weight/length^3; ±SE) of juvenile Chinook salmon deprived of food for 10 and 16 weeks and a control fed to satiation twice per week. Means were calculated from 30 fish/tank from 11/12 to 3/19, from tagged and untagged fish from 4/8 to 5/13, and from tagged fish after 5/13. An asterisk (*) near a marker indicates a significant difference ($p<0.05$) from the control on that date.

Hematocrit

The effect of deprivation on hematocrit levels in Chinook was not immediately apparent but a decrease was revealed in later months (Figure 14). The hematocrit levels of 10 week fish tended to have lower levels than the control throughout the study but were only significantly different from the control on July 8 ($F = 7.751$, $df = 2$, $p = 0.002$; Appendix 17). Hematocrit levels of 16 week fish were significantly lower than the control only on May 13 ($F = 6.334$, $p = 0.019$). Tank effect on hematocrit was significant on the on February 18 and April 8 ($F = 5.111$, $df = 9$, $p = 0.000$ and $F = 3.072$, $df = 9$, $p = 0.003$).

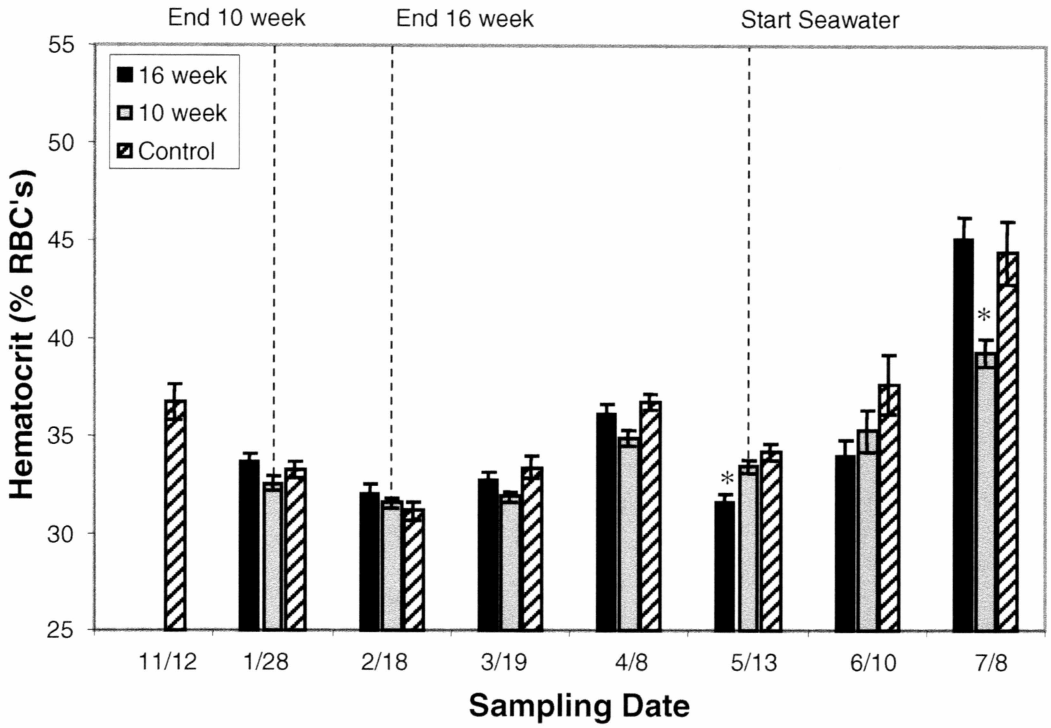

Figure 14: Mean hematocrit levels (% red blood cells; ±SE) of juvenile Chinook salmon deprived of food for 10 and 16 weeks and a control fed to satiation twice per week. Means were calculated from 10 fish per tank. An asterisk (*) above a column indicates a significant difference ($p<0.05$) from the control on that date.

Gill Na^+/K^+ ATPase

Food deprivation only affected gill ATPase activity in the 16 week fish on February 18 ($F = 5.089$, $p = 0.031$; Appendix 18; Figure 15). Tank effect was not significant at any time during the study.

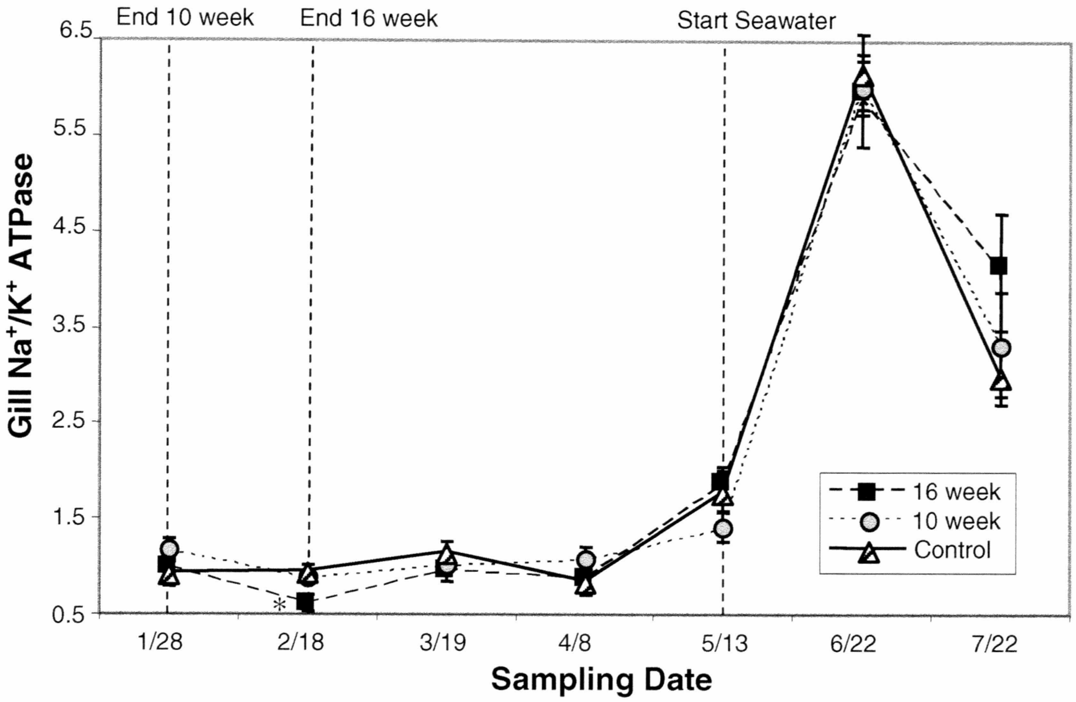

Figure 15: Mean gill Na^+/K^+ ATPase activity (μmoles ADP•mg $protein^{-1}$•$hour^{-1}$; ±SE) of juvenile Chinook salmon deprived of food for 10 and 16 weeks and a control fed to satiation twice per week. Means activity levels were calculated from 8 fish per treatment. An asterisk (*) near a marker indicates a significant difference ($p<0.05$) from the control on that date.

Proximate Composition

Whole-body lipid of all three groups decreased during the deprivation periods but the lipid content of treatment groups was not detectably different from the control at any time during the study ($F < 1.882$, $p > 0.208$; Appendix 19; Figure 16). Protein content was significantly lower in the 16 week fish on February 18 and May 13 ($F = 10.878$, $df = 1$, $p = 0.016$ and $F = 6.169$, $df = 2$, $p = 0.021$), but was not different from the control on July 22 ($F = 3.912$, $df = 2$, $p = 0.049$, Tukey's HSD: $p = 0.071$; Appendix 20; Figure 17).

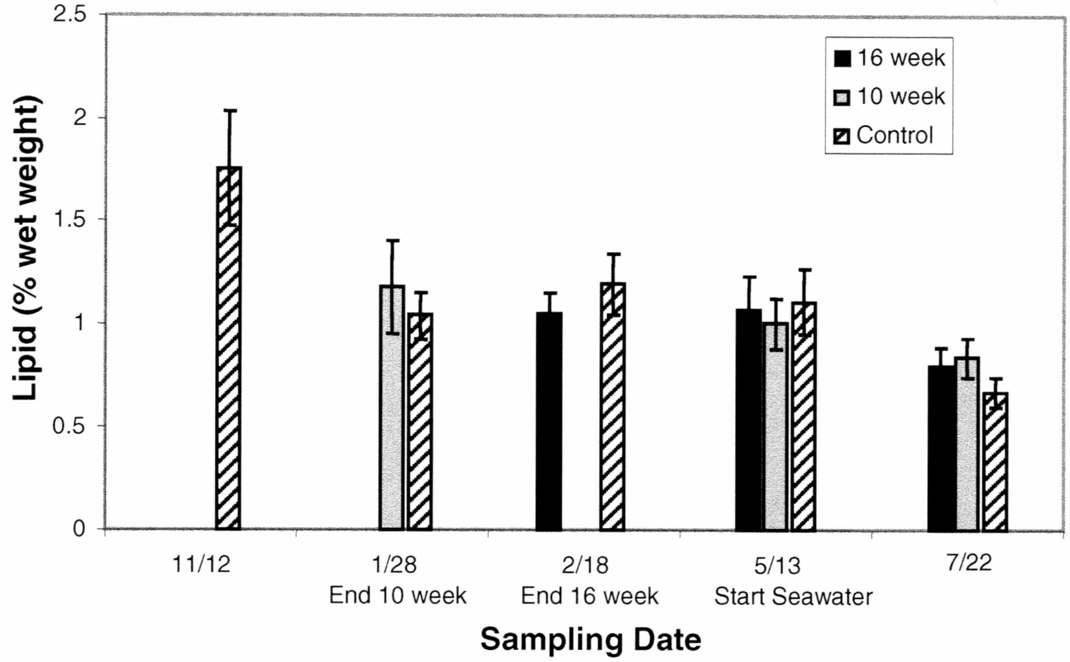

Figure 16: Mean whole-body lipid content (±SE) of juvenile Chinook salmon deprived of food for 10 and 16 weeks and a control fed to satiation twice per week. Means were calculated from 8 fish per treatment. Food deprivation did not have a significant effect on whole-body lipid content at any of the sampled time periods.

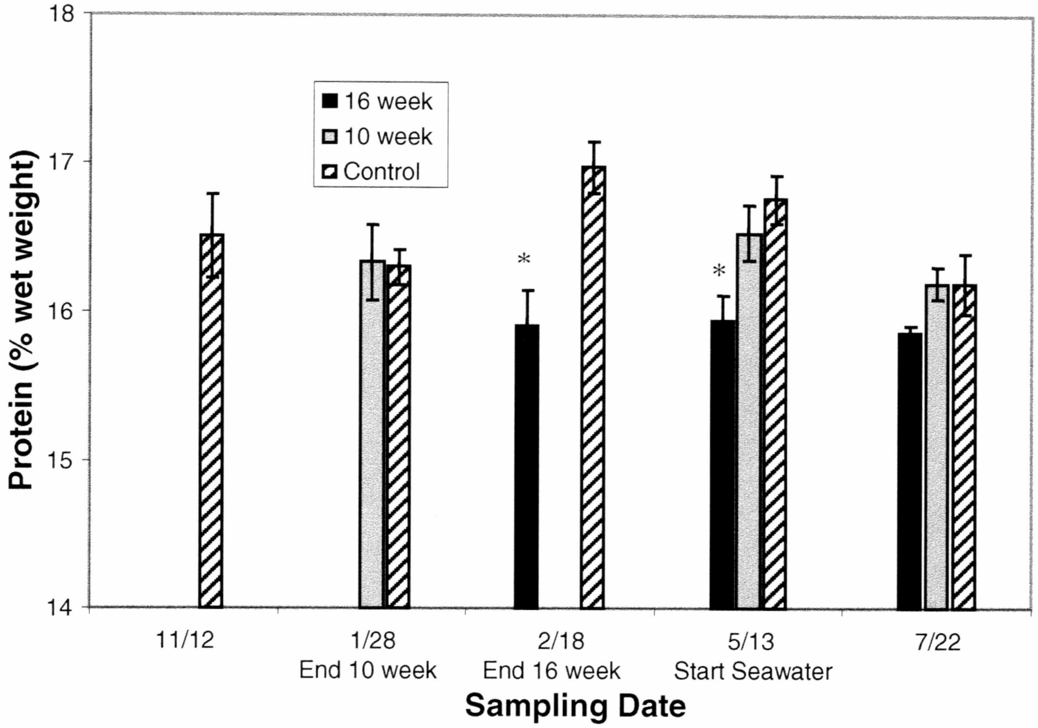

Figure 17: Mean protein content (±SE) of juvenile Chinook salmon deprived of food for 10 and 16 weeks and a control fed to satiation twice per week. Means were calculated from 8 fish per treatment. An asterisk (*) above a column indicates a significant difference ($p<0.05$) from the control on that date.

Moisture and ash content of both treatment groups was higher than the control after deprivation but only the 16 week fish had a significantly higher ash content ($F = 19.663$, $df = 1$, $p = 0.004$; Appendix 21 and 22; Figure 18 and 19) but ash content returned to control levels by May 13 ($F = 1.054$, $df = 2$, $p = 0.388$). Tank effect was only significant on ash content for the 10 week fish on January 28 ($F = 5.479$, $df = 6$, $p = 0.016$).

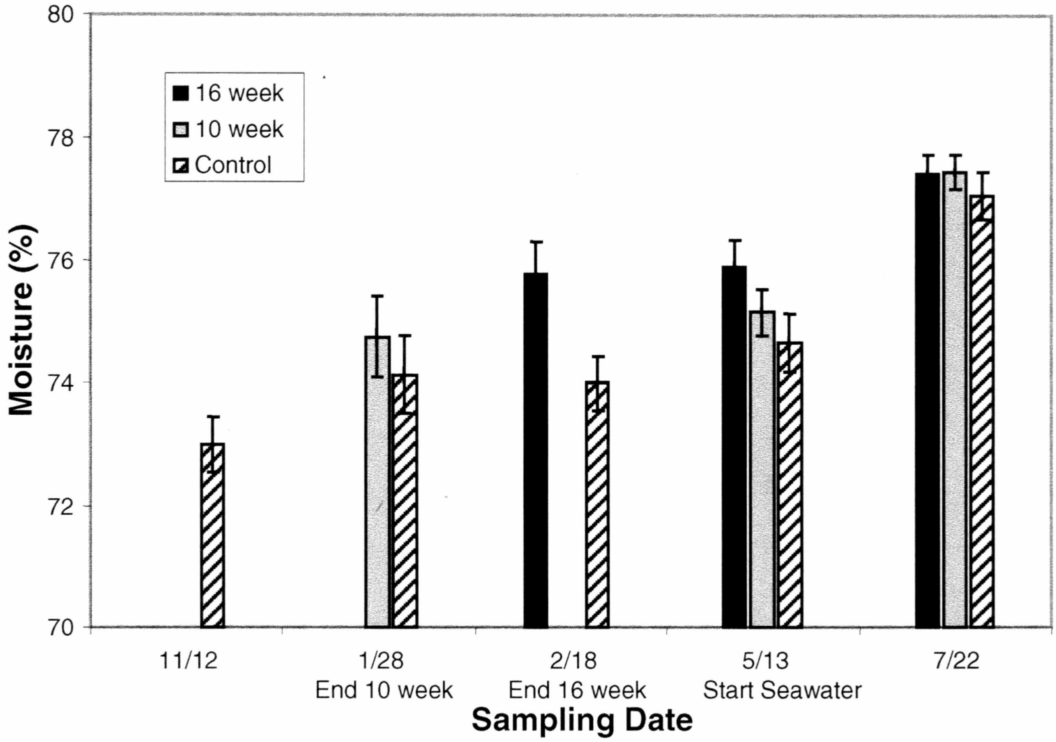

Figure 18: Mean moisture content (±SE) of juvenile Chinook salmon deprived of food for 10 and 16 weeks and a control fed to satiation twice per week. Means were calculated from 8 fish per treatment.

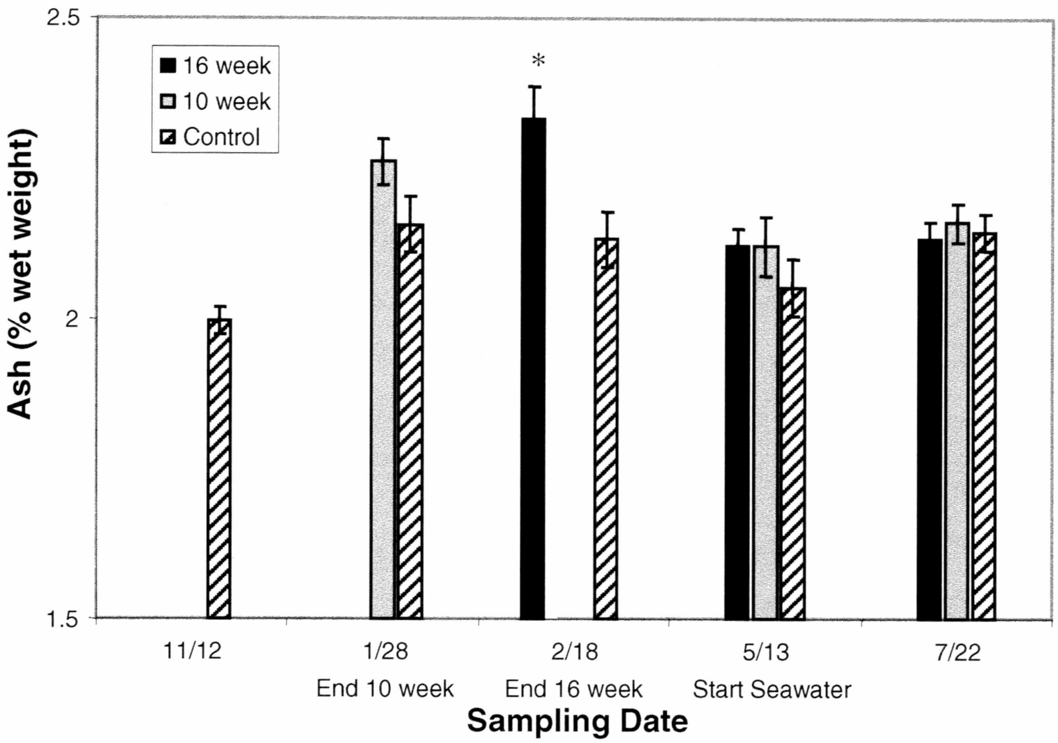

Figure 19: Mean ash content (±SE) of juvenile Chinook salmon deprived of food for 10 and 16 weeks and a control fed to satiation twice per week. Means were calculated from 8 fish per treatment. An asterisk (*) above a column indicates a significant difference ($p<0.05$) from the control on that date.

Male Maturation

On June 21, a malfunction of the seawater pump caused water circulation to stop and resulted in the loss of approximately two-thirds of the Chinook salmon. It was not apparent from dissecting the dead fish on June 22 whether there were any maturing males or not. Assuming that male and female smolts suffered equal losses and that half of the surviving fish were male, examination of the carcasses at the end of the study revealed a maturation rate of 8.57% (3 out of 35) for the control, 15.2% (5 out of 33) for the 10 week fish, and 13.5% (5 out of 37) for the 16 week fish.

Discussion

The results of this study agree with previous observations that salmonids offset the effects of unfavorable conditions by exhibiting either partial or full compensatory growth, typically consisting of elevated growth rates and rapid restoration of lost energy stores (Bilton and Robins 1973; Reimers et al. 1993; Hopkins and Unwin 1997; Nicieza and Metcalf 1997; Rumble 1997; Larsen et al. 2001a, 2001b; Nikki et al. 2003; Johnsson and Bohlin 2005). Compensatory growth is a mechanism for restricted fish to acquire the same growth trajectory as unrestricted fish and decrease the size variance in a population (Ali et al. 2003). Although most of the growth rates of the treatment fish in this study were not detectably different from the control fish after feeding resumed, they were significantly higher than the control after transfer to seawater. During freshwater rearing, cold water temperatures may have suppressed compensatory growth (Nicieza and Metcalfe 1997) so that a significant difference in growth rates was not detectable. The temperature of seawater at the time of transfer in May was approximately 3°C warmer than freshwater and would be expected to increase growth rates so that the difference between groups would be detectable.

As was expected, the 16 week fish of both species were more negatively affected by food deprivation than the 10 week fish in nearly all of the indices measured. All groups in this study experienced a decrease in lipid content over the winter, including the control, but only the 16 week coho showed a noticeable difference from the control and the difference may have been detectable with a larger number of samples. Protein content, however, was significantly affected by food deprivation and was easily detectable by ANOVA. The decrease in protein content was due to metabolism of protein during deprivation (Gardiner and Geddes 1980, Morgan et al. 2000) despite the fact that lipid reserves were not completely exhausted. The decrease in protein was most pronounced in the 16 week treatment groups, indicating that the additional six weeks of deprivation that occurred in November and February cost them a considerable amount of their energy reserves. The more substantial alterations of protein and lipid levels in the 16 week fish may have forced them to focus more on restoring body composition rather than growth (Morgan and Metcalfe 2001), which resulted in the smallest body size of the three groups at the end of the study.

The mean length and weight of the treatment fish were smaller than the control at the end of the study, the largest difference being between the 16 week and control fish (coho: 12.91cm vs. 13.25cm, 23.48g vs. 25.24g; Chinook: 13.58cm vs. 14.11cm, 32.82g vs. 36.50g), but it may not be large enough to affect the survival and size of the fish in the long-run if the rapid growth rates continue. Dickhoff et al. (1989) found that Atlantic salmon pre-smolts deprived of food in November and December were smaller at the time of release in the spring but after 4 months in seawater they were larger than controls. It is possible that the compensatory growth response was not fully observed during the time frame of the present study and the smaller, faster growing smolts could have caught up to or even surpassed the control smolts.

Hematocrit levels are a commonly used physiological test because deviations from control values can be a sign of health problems. The inconsistent response of hematocrit levels may have been caused by the relatively small number of samples taken. The unexpected decrease of hematocrit of 10 week fish for both species during the later part of the seawater rearing stage is most likely due to fact that the samples were obtained from ten fish from one tank per treatment, rather than as a result of food deprivation. If food deprivation was responsible for this decrease it would be expected that the 16 week fish would have experienced an even larger decrease, although that was not the case.

During the smolting process the plasma concentration of several hormones increase, including the stress hormone cortisol. Cortisol encourages growth and increases ATPase activity (Dickhoff et al. 1995) but at the same time it suppresses the immune system (Evans 1997). Rumble (1997) found that juvenile coho salmon subjected to an extended winter photoperiod grew faster in the spring and were larger than other photoperiod treatment groups but suffered higher mortality rates than other groups when infected with sea lice. The focus on compensatory growth after an extended winter photoperiod may have compounded the effects of the high levels of cortisol by diverting energy away from the immune system, causing the smolts to be more susceptible to parasitic infestation. A similar suppression of the immune system could occur in response to food deprivation, although there were no signs of it during this study.

Many physiological and morphological changes occur during the smolting process, two of which are an increase in ATPase activity and a decrease in condition factor (Dickhoff et al. 1995; Larsen et al. 2001a, 2001b). In this study, both of these events occurred near the middle of May, about a month later than what has been reported elsewhere. Many of these studies were conducted on populations at lower latitudes than Juneau, AK (longer photoperiod earlier in the year and warmer water temperatures) so those fish are more likely to have smolted earlier in the year than the fish in the present study. While it is possible that the fish were not fully smolted at the time of transfer to seawater, they had turned silver and very few died immediately after transfer which would suggest that the fish were close to completing the smolting process. The date of transfer to seawater was based on historic transfer dates at Macaulay Salmon Hatchery, which is, in turn, based on historical records of wild smolt out-migration in the Juneau area.

The decrease in ATPase activity observed near the end of the study in both species may have been caused by the salinity of the seawater in which they were being reared, rather than as a result of food deprivation, since it occurred in the control fish as well. Seawater was obtained from Gastineau Channel in front of the Macaulay Salmon Hatchery where salinities are strongly influenced by the phase of the tide cycle and the output of nearby freshwater streams. Salinity in this area can fluctuate between approximately 11 and 31, with a mean of approximately 23 during the seawater rearing stage of this study. This estuarine-like water may have caused the smolts to revert to parr (Folmar et al. 1982, Mortensen and Damsgard 1998, Stefansson et al. 1998), thereby reducing the ATPase activity of the fish. Even though juvenile salmonids may revert to parr status, they do not completely lose the ability to osmoregulate in seawater and quickly regain that ability after being transferred back to water with higher salinity (Mortensen and Damsgard 1998).

There was a detectable effect of Tank on growth despite efforts to replicate culture conditions in different tanks. Tank effect was more prevalent in coho than in Chinook, likely due to the locations of the tanks. The two species were grouped separately, with the coho closer to the work bench in the center of the lab and the Chinook closer to the back of the room. It is possible that the extra human activity in the work bench area caused more disturbances and additional stress to the coho that the Chinook did not experience, suppressing growth (Lankford and Weber 2006) and leading to larger variance between replicate tanks.

Maturation rates in this study should be interpreted with caution. This population of coho has a naturally low rate of early-maturing males so it was not surprising that no early-maturing males were found. Also, the rates of early-maturing Chinook reported above are most likely unreliable due to the loss of two-thirds of the fish before the end of the study. The rates of early-maturation reported for Chinook were based on the assumptions that equal numbers of immature and maturing males died when the seawater pump stopped and the sex ratio of the remaining fish was 1:1. No maturing males were apparent among the dead fish and histological examination of gonads was not conducted so the assumption of an equal sex ratio can not be validated. Furthermore, studies have shown that the period for determination of early male maturation in salmon smolts is in the fall before out-migration (Hopkins and Unwin 1997, Silverstein et al. 1998, Morgan and Metcalfe 2001, Larsen et al. 2006) so it was not expected that winter food deprivation would have as much of an affect on the number of early-maturing males as fall food restriction.

This study has shown that coho and Chinook smolts are able to compensate from food deprivation with little-to-no side effects, although the long-term effects on body size and marine survival remain unknown. Further research should include the evaluation of the deprivation feeding strategy in a hatchery setting. This will allow sufficient numbers of fish to be subjected to the food deprivation treatment to determine the effects on marine survival and growth and whether the results have practical significance. Not all of the physiological and morphological indices used in this study may be practical for use in a hatchery scale experiment, because of limitations due to cost, feasibility, technical expertise, etc. However, changes in weight, length, condition factor, and growth rates over time are commonly measured parameters in hatchery operations and appear to be good indicators of compensatory growth and would be a practical means of evaluating the effects food deprivation in hatchery pre-smolts.

Conclusion

Coho and Chinook pre-smolts in this study tolerated winter food deprivation without lasting effects on body composition, smolting ability, or condition factor, but the long-term effects on length and weight are unknown. Based on the majority of health indices observed in this study, food deprivation during the winter appears to be a viable option for increasing spring growth rates in hatchery produced coho and Chinook salmon smolts, which may, in turn, increase survival.

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Appendix 1: Summary of ANOVA's of length of coho parr deprived of food for 10 or 16 weeks in winter (treatments) or fed twice weekly to satiation (control).

Date of Sampling	ANOVA							Post Hoc	
	Source		Sum of Squares	df	Mean Square	F	Prob.	Control vs.	Prob.
11/19	Treatment	Hypothesis	1105162.079	2	552581.040	2.504	.136	10 week	.685
		Error	1991620.513	9.025	220682.980			16 week	.116
	Tank(Treatment)	Hypothesis	1987869.988	9	220874.443	1.631	.105		
		Error	50515529.319	373	135430.374				
1/28	Treatment	Hypothesis	12.512	2	6.256	7.912	.010	10 week	.041
		Error	7.122	9.007	.791			16 week	.011
	Tank(Treatment)	Hypothesis	7.122	9	.791	2.919	.002		
		Error	94.069	347	.271				
2/18	Treatment	Hypothesis	19.500	2	9.750	17.027	.001	10 week	.048
		Error	5.156	9.004	.573			16 week	.001
	Tank(Treatment)	Hypothesis	5.155	9	.573	1.860	.057		
		Error	106.528	346	.308				
3/19	Treatment	Hypothesis	1114885.329	2	557442.665	24.529	.000	10 week	.009
		Error	204577.186	9.002	22725.906			16 week	.000
	Tank(Treatment)	Hypothesis	204545.578	9	22727.286	1.564	.125		
		Error	4997563.126	344	14527.800				
4/8	Treatment	Hypothesis	12273.651	2	6136.825	29.827	.000	10 week	.013
		Error	1852.362	9.003	205.744			16 week	.000
	Tank(Treatment)	Hypothesis	1852.234	9	205.804	2.614	.006		
		Error	59040.768	750	78.721				
5/13	Treatment	Hypothesis	46.842	2	23.421	22.086	.000	10 week	.043
		Error	9.645	9.096	1.060			16 week	.000
	Tank(Treatment)	Hypothesis	9.655	9	1.073	3.208	.001		
		Error	318.988	954	.334				

Appendix 1 continued: Summary of ANOVA's of length of coho parr deprived of food for 10 or 16 weeks in winter (treatments) or fed twice weekly to satiation (control).

Date of Sampling	ANOVA							Post Hoc	
	Source		**Sum of Squares**	**df**	**Mean Square**	**F**	**Prob.**	**Control vs.**	**Prob.**
5/27	Treatment	Hypothesis	15.150	2	7.575	12.756	.002	10 week	.069
		Error	5.372	9.047	.594			16 week	.002
	Tank(Treatment)	Hypothesis	5.364	9	.596	2.397	.011		
		Error	131.048	527	.249				
6/10	Treatment	Hypothesis	10.317	2	5.159	6.212	.020	10 week	.400
		Error	7.480	9.007	.830			16 week	.016
	Tank(Treatment)	Hypothesis	7.479	9	.831	2.912	.002		
		Error	145.242	509	.285				
6/22	Treatment	Hypothesis	7.706	2	3.853	5.368	.029	10 week	.321
		Error	6.469	9.012	.718			16 week	.023
	Tank(Treatment)	Hypothesis	6.465	9	.718	2.089	.029		
		Error	177.086	515	.344				
7/8	Treatment	Hypothesis	9.471	2	4.736	6.314	.019	10 week	.187
		Error	6.762	9.017	.750			16 week	.014
	Tank(Treatment)	Hypothesis	6.753	9	.750	1.526	.135		
		Error	252.227	513	.492				
7/22	Treatment	Hypothesis	9.400	2	4.700	4.681	.040	10 week	.215
		Error	9.058	9.020	1.004			16 week	.030
	Tank(Treatment)	Hypothesis	9.042	9	1.005	1.442	.167		
		Error	356.036	511	.697				

Appendix 2: Summary of ANOVA's of weight of coho parr deprived of food for 10 or 16 weeks in winter (treatments) or fed twice weekly to satiation (control).

Date of Sampling	ANOVA							Post Hoc	
	Source		Sum of Squares	df	Mean Square	F	Prob.	Control vs.	Prob.
11/19	Treatment	Hypothesis	66.733	2	33.367	11.245	.004	10 week	.967
		Error	26.764	9.020	2.967			16 week	.007
	Tank(Treatment)	Hypothesis	26.729	9	2.970	1.811	.065		
		Error	616.649	376	1.640				
1/28	Treatment	Hypothesis	165.211	2	82.605	17.851	.001	10 week	.004
		Error	41.666	9.004	4.628			16 week	.001
	Tank(Treatment)	Hypothesis	41.668	9	4.630	3.295	.001		
		Error	486.109	346	1.405				
2/18	Treatment	Hypothesis	309.275	2	154.638	35.419	.000	10 week	.016
		Error	39.311	9.004	4.366			16 week	.000
	Tank(Treatment)	Hypothesis	39.311	9	4.368	2.985	.002		
		Error	497.514	340	1.463				
3/19	Treatment	Hypothesis	256.655	2	128.328	34.700	.000	10 week	.004
		Error	33.284	9	3.698			16 week	.000
	Tank(Treatment)	Hypothesis	33.284	9	3.698	1.948	.045		
		Error	660.558	348	1.898				
4/8	Treatment	Hypothesis	482.738	2	241.369	46.544	.000	10 week	.006
		Error	46.676	9.001	5.186			16 week	.000
	Tank(Treatment)	Hypothesis	46.675	9	5.186	2.604	.006		
		Error	1517.782	762	1.992				
5/13	Treatment	Hypothesis	526.263	2	263.131	31.707	.000	10 week	.016
		Error	75.549	9.103	8.299			16 week	.000
	Tank(Treatment)	Hypothesis	75.529	9	8.392	2.970	.002		
		Error	2695.275	954	2.825				

Appendix 2 continued: Summary of ANOVA's of weight of coho parr deprived of food for 10 or 16 weeks in winter (treatments) or fed twice weekly to satiation (control).

Date of Sampling	ANOVA							Post Hoc	
	Source		Sum of Squares	df	Mean Square	F	Prob.	Control vs.	Prob.
5/27	Treatment	Hypothesis	166.363	2	83.182	19.891	.000	10 week	.019
		Error	37.937	9.072	4.182			16 week	.000
	Tank(Treatment)	Hypothesis	37.719	9	4.191	1.547	.128		
		Error	1427.836	527	2.709				
6/10	Treatment	Hypothesis	153.794	2	76.897	14.080	.002	10 week	.240
		Error	49.252	9.018	5.461			16 week	.001
	Tank(Treatment)	Hypothesis	49.175	9	5.464	1.460	.160		
		Error	1904.924	509	3.742				
6/22	Treatment	Hypothesis	177.416	2	88.708	11.000	.004	10 week	.146
		Error	72.708	9.016	8.064			16 week	.003
	Tank(Treatment)	Hypothesis	72.607	9	8.067	1.418	.177		
		Error	2923.775	514	5.688				
7/8	Treatment	Hypothesis	224.207	2	112.104	8.763	.008	10 week	.142
		Error	115.351	9.017	12.792			16 week	.006
	Tank(Treatment)	Hypothesis	115.146	9	12.794	1.143	.331		
		Error	5755.843	514	11.198				
7/22	Treatment	Hypothesis	272.192	2	136.096	3.980	.058	10 week	.223
		Error	308.223	9.013	34.198			16 week	.048
	Tank(Treatment)	Hypothesis	307.959	9	34.218	1.812	.064		
		Error	9612.286	509	18.885				

Appendix 3: Summary of ANOVA's of length specific growth rates of coho parr deprived of food for 10 or 16 weeks in winter (treatments) or fed twice weekly to satiation (control).

Dates	ANOVA							Post Hoc	
	Source		**Sum of Squares**	**df**	**Mean Square**	**F**	**Prob.**	**Control vs.**	**Prob.**
11/19 – 1/28	Treatment	Hypothesis	.005	2	.002	3.939	.059	10 week	.088
		Error	.006	9	.001			16 week	.087
1/28 – 2/18	Treatment	Hypothesis	.025	2	.012	1.655	.244	10 week	.840
		Error	.068	9	.008			16 week	.476
2/18 – 3/19	Treatment	Hypothesis	.001	2	.001	.135	.876	10 week	.870
		Error	.038	9	.004			16 week	.988
3/19 – 4/8	Treatment	Hypothesis	.006	2	.003	.505	.619	10 week	.625
		Error	.057	9	.006			16 week	.734
4/8 – 5/13	Treatment	Hypothesis	.000	2	.000	.181	.837	10 week	.974
		Error	.007	9	.001			16 week	.826
5/13 – 5/27	Treatment	Hypothesis	.900	2	.450	13.484	.002	10 week	.058
		Error	.302	9.039	.033			16 week	.001
	Tank(Treatment)	Hypothesis	.301	9	.033	2.647	.005		
		Error	6.481	512	.013				
5/27 – 6/10	Treatment	Hypothesis	.397	2	.199	18.129	.001	10 week	.036
		Error	.100	9.085	.011			16 week	.001
	Tank(Treatment)	Hypothesis	.099	9	.011	1.910	.049		
		Error	2.403	417	.006				
6/10 – 6/22	Treatment	Hypothesis	.154	2	.077	9.571	.006	10 week	.912
		Error	.073	9.046	.008			16 week	.015
	Tank(Treatment)	Hypothesis	.072	9	.008	1.028	.416		
		Error	3.824	488	.008				

Appendix 3 continued: Summary of ANOVA's of length specific growth rates of coho parr deprived of food for 10 or 16 weeks in winter (treatments) or fed twice weekly to satiation (control).

Dates of Sampling	**ANOVA**							**Post Hoc**	
	Source		**Sum of Squares**	**df**	**Mean Square**	**F**	**Prob.**	**Control vs.**	**Prob.**
6/22 – 7/8	Treatment	Hypothesis	.042	2	.021	1.456	.283	10 week	.658
		Error	.129	9.018	.014			16 week	.682
	Tank(Treatment)	Hypothesis	.128	9	.014	1.687	.089		
		Error	4.235	501	.008				
7/8 – 7/22	Treatment	Hypothesis	.065	2	.033	2.596	.128	10 week	.100
		Error	.114	9.086	.013			16 week	.316
	Tank(Treatment)	Hypothesis	.113	9	.013	.914	.513		
		Error	6.630	483	.014				

Appendix 4: Summary of ANOVA's of weight specific growth rates of coho parr deprived of food for 10 or 16 weeks in winter (treatments) or fed twice weekly to satiation (control).

Dates of Sampling	ANOVA							Post Hoc	
	Source		**Sum of Squares**	**df**	**Mean Square**	**F**	**Prob.**	**Control vs.**	**Prob.**
11/19 – 1/28	Treatment	Hypothesis	.160	2	.080	10.554	.004	10 week	.004
		Error	.068	9	.008			16 week	.047
1/28 – 2/18	Treatment	Hypothesis	1.302	2	.651	7.268	.013	10 week	.522
		Error	.806	9	.090			16 week	.069
2/18 – 3/19	Treatment	Hypothesis	.195	2	.098	1.988	.193	10 week	.986
		Error	.442	9	.049			16 week	.279
3/19 – 4/8	Treatment	Hypothesis	.128	2	.064	1.694	.237	10 week	.259
		Error	.339	9	.038			16 week	.349
4/8 – 5/13	Treatment	Hypothesis	.046	2	.023	4.690	.040	10 week	.745
		Error	.044	9	.005			16 week	.039
5/13 – 5/27	Treatment	Hypothesis	18.249	2	9.125	21.493	.000	10 week	.020
		Error	3.835	9.034	.425			16 week	.000
	Tank(Treatment)	Hypothesis	3.837	9	.426	3.272	.001		
		Error	66.451	510	.130				
5/27 – 6/10	Treatment	Hypothesis	3.009	2	1.504	14.874	.001	10 week	.035
		Error	.918	9.080	.101			16 week	.001
	Tank(Treatment)	Hypothesis	.914	9	.102	1.809	.065		
		Error	23.511	419	.056				
6/10 – 6/22	Treatment	Hypothesis	2.421	2	1.210	40.103	.000	10 week	.851
		Error	.274	9.084	.030			16 week	.000
	Tank(Treatment)	Hypothesis	.271	9	.030	.457	.903		
		Error	32.028	486	.066				

Appendix 4 continued: Summary of ANOVA's of weight specific growth rates of coho parr deprived of food for 10 or 16 weeks in winter (treatments) or fed twice weekly to satiation (control).

Dates of Sampling	**ANOVA**							**Post Hoc**	
	Source		**Sum of Squares**	**df**	**Mean Square**	**F**	**Prob.**	**Control vs.**	**Prob.**
6/22 – 7/8	Treatment	Hypothesis	15.464	2	7.732	7.437	.012	10 week	.957
		Error	9.370	9.012	1.040			16 week	.019
	Tank(Treatment)	Hypothesis	9.361	9	1.040	1.614	.108		
		Error	317.664	493	.644				
7/8 – 7/22	Treatment	Hypothesis	3.990	2	1.995	2.564	.131	10 week	.907
		Error	7.019	9.020	.778			16 week	.265
	Tank(Treatment)	Hypothesis	7.003	9	.778	.886	.537		
		Error	429.355	489	.878				

Appendix 5: Summary of ANOVA's of condition factor of coho parr deprived of food for 10 or 16 weeks in winter (treatments) or fed twice weekly to satiation (control).

Date of Sampling	ANOVA							Post Hoc	
	Source		**Sum of Squares**	**df**	**Mean Square**	**F**	**Prob.**	**Control vs.**	**Prob.**
11/19	Treatment	Hypothesis	.599	2	.299	158.945	.000	10 week	.032
		Error	.017	9.059	.002			16 week	.000
	Tank(Treatment)	Hypothesis	.017	9	.002	.592	.804		
		Error	1.147	361	.003				
1/28	Treatment	Hypothesis	1.009	2	.504	47.246	.000	10 week	.000
		Error	.096	9.020	.011			16 week	.000
	Tank(Treatment)	Hypothesis	.096	9	.011	2.675	.005		
		Error	1.352	338	.004				
2/18	Treatment	Hypothesis	1.878	2	.939	121.099	.000	10 week	.004
		Error	.070	9.005	.008			16 week	.000
	Tank(Treatment)	Hypothesis	.070	9	.008	2.923	.002		
		Error	.884	333	.003				
3/19	Treatment	Hypothesis	7.021	2	3.510	36.261	.000	10 week	.012
		Error	.871	9.001	.097			16 week	.000
	Tank(Treatment)	Hypothesis	.871	9	.097	3.318	.001		
		Error	9.923	340	.029				
4/8	Treatment	Hypothesis	.570	2	.285	34.390	.000	10 week	.039
		Error	.075	9.003	.008			16 week	.000
	Tank(Treatment)	Hypothesis	.075	9	.008	3.046	.001		
		Error	1.975	726	.003				
5/13	Treatment	Hypothesis	.246	2	.123	7.594	.012	10 week	.425
		Error	.147	9.065	.016			16 week	.012
	Tank(Treatment)	Hypothesis	.148	9	.016	4.712	.000		
		Error	3.327	954	.003				

Appendix 5 continued: Summary of ANOVA's of condition factor of coho parr deprived of food for 10 or 16 weeks in winter (treatments) or fed twice weekly to satiation (control).

Date of Sampling	ANOVA							Post Hoc	
	Source		Sum of Squares	df	Mean Square	F	Prob.	Control vs.	Prob.
5/27	Treatment	Hypothesis	.023	2	.011	4.576	.042	10 week	.198
		Error	.023	9.081	.002			16 week	.037
	Tank(Treatment)	Hypothesis	.022	9	.002	1.169	.312		
		Error	1.097	514	.002				
6/10	Treatment	Hypothesis	.020	2	.010	9.564	.006	10 week	.118
		Error	.010	9.038	.001			16 week	.005
	Tank(Treatment)	Hypothesis	.010	9	.001	.735	.677		
		Error	.703	485	.001				
6/22	Treatment	Hypothesis	.014	2	.007	4.811	.038	10 week	.426
		Error	.013	9.035	.001			16 week	.032
	Tank(Treatment)	Hypothesis	.013	9	.001	.767	.647		
		Error	.980	506	.002				
7/8	Treatment	Hypothesis	.001	2	.000	.127	.882	10 week	.921
		Error	.021	9.019	.002			16 week	.886
	Tank(Treatment)	Hypothesis	.021	9	.002	.986	.451		
		Error	1.199	505	.002				
7/22	Treatment	Hypothesis	.035	2	.017	1.676	.241	10 week	.464
		Error	.093	9.021	.010			16 week	.208
	Tank(Treatment)	Hypothesis	.093	9	.010	1.422	.176		
		Error	3.558	489	.007				

Appendix 6: Summary of ANOVA's of hematocrit of coho parr deprived of food for 10 or 16 weeks in winter (treatments) or fed twice weekly to satiation (control).

Date of Sampling	ANOVA							Post Hoc	
	Source		Sum of Squares	df	Mean Square	F	Prob.	Control vs.	Prob.
1/28	Treatment	Hypothesis	913261.229	2	456630.615	4.710	.045	10 week	.146
		Error	774825.593	7.993	96941.351			16 week	.033
	Tank(Treatment)	Hypothesis	775157.220	8	96894.653	2.059	.048		
		Error	4282794.917	91	47063.680				
2/18	Treatment	Hypothesis	404.874	2	202.437	3.259	.092	10 week	.312
		Error	497.364	8.006	62.124			16 week	.082
	Tank(Treatment)	Hypothesis	498.561	8	62.320	9.365	.000		
		Error	645.478	97	6.654				
3/19	Treatment	Hypothesis	381.549	2	190.775	8.037	.015	10 week	.029
		Error	166.333	7.007	23.738			16 week	.020
	Tank(Treatment)	Hypothesis	166.552	7	23.793	5.627	.000		
		Error	376.300	89	4.228				
4/8	Treatment	Hypothesis	298.987	2	149.494	1.921	.202	10 week	.801
		Error	700.388	9.001	77.812			16 week	.184
	Tank(Treatment)	Hypothesis	700.649	9	77.850	9.369	.000		
		Error	889.100	107	8.309				
5/13	Treatment	Hypothesis	155.017	2	77.508	.662	.539	10 week	.889
		Error	1053.229	9.001	117.016			16 week	.784
	Tank(Treatment)	Hypothesis	1053.683	9	117.076	13.945	.000		
		Error	898.300	107	8.395				
6/10	Treatment	Hypothesis	174.867	2	87.433	7.284	.003	10 week	.046
		Error	324.100	27	12.004			16 week	.448
7/8	Treatment	Hypothesis	361.667	2	180.833	9.252	.001	10 week	.001
		Error	527.700	27	19.544			16 week	.731

Appendix 7: Summary of ANOVA's of gill Na^+/K^+ ATPase activity of coho parr deprived of food for 10 or 16 weeks in winter (treatments) or fed twice weekly to satiation (control).

Date of Sampling	ANOVA							Post Hoc	
	Source		Sum of Squares	df	Mean Square	F	Prob.	Control vs.	Prob.
1/28	Treatment	Hypothesis	.303	2	.151	.826	.468	10 week	.439
		Error	1.650	9	.183			16 week	.838
	Tank(Treatment)	Hypothesis	1.650	9	.183	2.449	.075		
		Error	.898	12	.075				
2/18	Treatment	Hypothesis	.267	2	.134	.567	.586	10 week	.750
		Error	2.121	9	.236			16 week	.952
	Tank(Treatment)	Hypothesis	2.121	9	.236	4.169	.012		
		Error	.678	12	.057				
3/19	Treatment	Hypothesis	1.259	2	.630	14.129	.001	10 week	.001
		Error	.471	10.575	.045			16 week	.015
	Tank(Treatment)	Hypothesis	.378	9	.042	.293	.962		
		Error	1.575	11	.143				
4/8	Treatment	Hypothesis	1.301	2	.650	2.374	.148	10 week	.204
		Error	2.514	9.181	.274			16 week	.325
	Tank(Treatment)	Hypothesis	2.495	9	.277	2.249	.075		
		Error	1.973	16	.123				
5/13	Treatment	Hypothesis	.061	2	.030	.893	.443	10 week	.456
		Error	.305	9	.034			16 week	.575
	Tank(Treatment)	Hypothesis	.305	9	.034	.940	.527		
		Error	.433	12	.036				
6/10	Treatment	Hypothesis	3.237	2	1.618	.917	.415	10 week	.389
		Error	37.068	21	1.765			16 week	.686
7/8	Treatment	Hypothesis	6.075	2	3.038	1.366	.277	10 week	.450
		Error	46.699	21	2.224			16 week	.279

Appendix 8: Summary of ANOVA's of whole-body lipid content of coho parr deprived of food for 10 or 16 weeks in winter (treatments) or fed twice weekly to satiation (control).

Date of Sampling	ANOVA							Post Hoc	
	Source		**Sum of Squares**	**df**	**Mean Square**	**F**	**Prob.**	**Control vs.**	**Prob.**
1/28	Treatment	Hypothesis	.000	1	.000	.368	.566		
		Error	.007	6	.001				
	Tank(Treatment)	Hypothesis	.007	6	.001	1.846	.207		
		Error	.005	8	.001				
2/18	Treatment	Hypothesis	.003	1	.003	5.383	.056		
		Error	.003	6.505	.000				
	Tank(Treatment)	Hypothesis	.003	6	.000	1.062	.463		
		Error	.003	7	.000				
5/13	Treatment	Hypothesis	9.06E-005	2	4.53E-005	.069	.934	10 week	1.000
		Error	.006	9	.001			16 week	.948
	Tank(Treatment)	Hypothesis	.006	9	.001	1.584	.225		
		Error	.005	12	.000				
7/22	Treatment	Hypothesis	2.68E-005	2	1.34E-005	.029	.972	10 week	.998
		Error	.004	9	.000			16 week	.971
	Tank(Treatment)	Hypothesis	.004	9	.000	2.169	.106		
		Error	.003	12	.000				

Appendix 9: Summary of ANOVA's of protein content of coho parr deprived of food for 10 or 16 weeks in winter (treatments) or fed twice weekly to satiation (control).

Date of Sampling	ANOVA							Post Hoc	
	Source		**Sum of Squares**	**df**	**Mean Square**	**F**	**Prob.**	**Control vs.**	**Prob.**
1/28	Treatment	Hypothesis	1.048	1	1.048	1.515	.264		
		Error	4.151	6	.692				
	Tank(Treatment)	Hypothesis	4.151	6	.692	4.819	.023		
		Error	1.149	8	.144				
2/18	Treatment	Hypothesis	5.953	1	5.953	22.287	.003		
		Error	1.603	6	.267				
	Tank(Treatment)	Hypothesis	1.603	6	.267	1.209	.391		
		Error	1.768	8	.221				
5/13	Treatment	Hypothesis	2.087	2	1.043	5.991	.022	10 week	.093
		Error	1.567	9	.174			16 week	.021
	Tank(Treatment)	Hypothesis	1.567	9	.174	.731	.676		
		Error	2.859	12	.238				
7/22	Treatment	Hypothesis	.409	2	.205	.719	.513	10 week	.940
		Error	2.562	9	.285			16 week	.501
	Tank(Treatment)	Hypothesis	2.562	9	.285	1.425	.278		
		Error	2.396	12	.200				

Appendix 10: Summary of ANOVA's of moisture content of coho parr deprived of food for 10 or 16 weeks in winter (treatments) or fed twice weekly to satiation (control).

Date of Sampling	**ANOVA**							**Post Hoc**	
	Source		**Sum of Squares**	**df**	**Mean Square**	**F**	**Prob.**	**Control vs.**	**Prob.**
1/28	Treatment	Hypothesis	1.766	1	1.766	2.859	.142		
		Error	3.705	6	.618				
	Tank(Treatment)	Hypothesis	3.705	6	.618	.835	.575		
		Error	5.919	8	.740				
2/18	Treatment	Hypothesis	32.991	1	32.991	52.492	.000		
		Error	3.771	6	.628				
	Tank(Treatment)	Hypothesis	3.771	6	.628	.737	.635		
		Error	6.819	8	.852				
5/13	Treatment	Hypothesis	.016	2	.008	1.671	.241	10 week	.853
		Error	.043	9	.005			16 week	.229
	Tank(Treatment)	Hypothesis	.043	9	.005	1.568	.230		
		Error	.037	12	.003				
7/22	Treatment	Hypothesis	.623	2	.312	.635	.555	10 week	.684
		Error	3.927	8	.491			16 week	.569
	Tank(Treatment)	Hypothesis	3.927	8	.491	.963	.508		
		Error	5.608	11	.510				

Appendix 11: Summary of ANOVA's of ash content of coho parr deprived of food for 10 or 16 weeks in winter (treatments) or fed twice weekly to satiation (control).

Date of Sampling	ANOVA							Post Hoc	
	Source		Sum of Squares	df	Mean Square	F	Prob.	Control vs.	Prob.
1/28	Treatment	Hypothesis	.069	1	.069	6.158	.048		
		Error	.067	6	.011				
	Tank(Treatment)	Hypothesis	.067	6	.011	.997	.487		
		Error	.090	8	.011				
2/18	Treatment	Hypothesis	.254	1	.254	37.505	.001		
		Error	.041	6	.007				
	Tank(Treatment)	Hypothesis	.041	6	.007	1.047	.462		
		Error	.052	8	.006				
5/13	Treatment	Hypothesis	.055	2	.028	1.805	.219	10 week	1.000
		Error	.137	9	.015			16 week	.275
	Tank(Treatment)	Hypothesis	.137	9	.015	1.589	.224		
		Error	.115	12	.010				
7/22	Treatment	Hypothesis	.386	2	.193	.955	.421	10 week	.409
		Error	1.817	9	.202			16 week	.923
	Tank(Treatment)	Hypothesis	1.817	9	.202	.633	.750		
		Error	3.825	12	.319				

Appendix 12: Summary of ANOVA's of length of Chinook parr deprived of food for 10 or 16 weeks in winter (treatments) or fed twice weekly to satiation (control).

Date of Sampling	ANOVA							Post Hoc	
	Source		Sum of Squares	df	Mean Square	F	Prob.	Control vs.	Prob.
11/19	Treatment	Hypothesis	753.846	2	376.923	1.929	.201	10 week	.826
		Error	1761.966	9.015	195.443			16 week	.475
	Tank(Treatment)	Hypothesis	1760.327	9	195.592	1.901	.051		
		Error	37655.135	366	102.883				
1/28	Treatment	Hypothesis	11.776	2	5.888	14.762	.001	10 week	.289
		Error	3.592	9.005	.399			16 week	.001
	Tank(Treatment)	Hypothesis	3.590	9	.399	1.439	.170		
		Error	93.972	339	.277				
2/18	Treatment	Hypothesis	10.723	2	5.362	48.698	.000	10 week	.526
		Error	.992	9.008	.110			16 week	.000
	Tank(Treatment)	Hypothesis	.991	9	.110	.375	.947		
		Error	100.960	344	.293				
3/19	Treatment	Hypothesis	.306	2	.153	62.175	.000	10 week	.007
		Error	.022	9.016	.002			16 week	.000
	Tank(Treatment)	Hypothesis	.022	9	.002	.371	.948		
		Error	2.272	343	.007				
4/8	Treatment	Hypothesis	14.966	2	7.483	29.158	.000	10 week	.022
		Error	2.311	9.003	.257			16 week	.000
	Tank(Treatment)	Hypothesis	2.310	9	.257	.925	.502		
		Error	208.284	751	.277				
5/13	Treatment	Hypothesis	29.372	2	14.686	27.312	.000	10 week	.027
		Error	4.945	9.196	.538			16 week	.000
	Tank(Treatment)	Hypothesis	4.865	9	.541	1.493	.146		
		Error	362.835	1002	.362				

Appendix 12 continued: Summary of ANOVA's of length of Chinook parr deprived of food for 10 or 16 weeks in winter (treatments) or fed twice weekly to satiation (control).

Date of Sampling	ANOVA							Post Hoc	
	Source		Sum of Squares	df	Mean Square	F	Prob.	Control vs.	Prob.
5/27	Treatment	Hypothesis	7301.971	2	3650.986	22.386	.000	10 week	.033
		Error	1468.483	9.004	163.091			16 week	.000
	Tank(Treatment)	Hypothesis	1467.822	9	163.091	1.021	.421		
		Error	101592.730	636	159.737				
6/10	Treatment	Hypothesis	6309.575	2	3154.788	15.606	.001	10 week	.101
		Error	1821.810	9.012	202.156			16 week	.001
	Tank(Treatment)	Hypothesis	1819.447	9	202.161	1.032	.412		
		Error	122216.334	624	195.860				
6/22	Treatment	Hypothesis	10.329	2	5.165	8.310	.008	10 week	.200
		Error	6.166	9.921	.621			16 week	.005
	Tank(Treatment)	Hypothesis	5.630	9	.626	1.138	.338		
		Error	104.425	190	.550				
7/8	Treatment	Hypothesis	9.737	2	4.869	6.279	.018	10 week	.335
		Error	7.490	9.659	.775			16 week	.012
	Tank(Treatment)	Hypothesis	7.022	9	.780	1.179	.310		
		Error	128.355	194	.662				
7/22	Treatment	Hypothesis	10.625	2	5.312	6.576	.015	10 week	.547
		Error	7.959	9.852	.808			16 week	.015
	Tank(Treatment)	Hypothesis	7.311	9	.812	1.125	.347		
		Error	137.970	191	.722				

Appendix 13: Summary of ANOVA's of weight of Chinook parr deprived of food for 10 or 16 weeks in winter (treatments) or fed twice weekly to satiation (control).

Date of Sampling	ANOVA							Post Hoc	
	Source		Sum of Squares	df	Mean Square	F	Prob.	Control vs.	Prob.
11/19	Treatment	Hypothesis	88.147	2	44.073	16.617	.001	10 week	.962
		Error	23.980	9.041	2.652			16 week	.002
	Tank(Treatment)	Hypothesis	23.858	9	2.651	.765	.649		
		Error	1271.702	367	3.465				
1/28	Treatment	Hypothesis	337.677	2	168.838	49.324	.000	10 week	.002
		Error	30.841	9.010	3.423			16 week	.000
	Tank(Treatment)	Hypothesis	30.808	9	3.423	1.016	.427		
		Error	1149.006	341	3.370				
2/18	Treatment	Hypothesis	356.938	2	178.469	74.392	.000	10 week	.106
		Error	21.604	9.005	2.399			16 week	.000
	Tank(Treatment)	Hypothesis	21.590	9	2.399	.753	.660		
		Error	1079.311	339	3.184				
3/19	Treatment	Hypothesis	.148	2	.074	57.421	.000	10 week	.011
		Error	.012	9.006	.001			16 week	.000
	Tank(Treatment)	Hypothesis	.012	9	.001	.908	.518		
		Error	.488	343	.001				
4/8	Treatment	Hypothesis	12.902	2	6.451	52.378	.000	10 week	.008
		Error	1.109	9.003	.123			16 week	.000
	Tank(Treatment)	Hypothesis	1.109	9	.123	1.286	.241		
		Error	71.762	749	.096				
5/13	Treatment	Hypothesis	582.878	2	291.439	29.474	.000	10 week	.028
		Error	90.483	9.151	9.888			16 week	.000
	Tank(Treatment)	Hypothesis	89.652	9	9.961	1.895	.049		
		Error	5250.967	999	5.256				

Appendix 13 continued: Summary of ANOVA's of weight of Chinook parr deprived of food for 10 or 16 weeks in winter (treatments) or fed twice weekly to satiation (control).

Date of Sampling	ANOVA							Post Hoc	
	Source		Sum of Squares	df	Mean Square	F	Prob.	Control vs.	Prob.
5/27	Treatment	Hypothesis	6.178	2	3.089	20.399	.000	10 week	.051
		Error	1.363	9.003	.151			16 week	.000
	Tank(Treatment)	Hypothesis	1.363	9	.151	1.097	.363		
		Error	87.667	635	.138				
6/10	Treatment	Hypothesis	5.637	2	2.819	12.628	.002	10 week	.172
		Error	2.010	9.005	.223			16 week	.002
	Tank(Treatment)	Hypothesis	2.009	9	.223	1.410	.180		
		Error	99.234	627	.158				
6/22	Treatment	Hypothesis	177.416	2	88.708	11.000	.004	10 week	.146
		Error	72.708	9.016	8.064			16 week	.003
	Tank(Treatment)	Hypothesis	72.607	9	8.067	1.418	.177		
		Error	2923.775	514	5.688				
7/8	Treatment	Hypothesis	2.900	2	1.450	4.546	.040	10 week	.441
		Error	3.099	9.715	.319			16 week	.026
	Tank(Treatment)	Hypothesis	2.881	9	.320	1.088	.373		
		Error	57.051	194	.294				
7/22	Treatment	Hypothesis	467.855	2	233.928	5.901	.020	10 week	.438
		Error	402.676	10.158	39.642			16 week	.017
	Tank(Treatment)	Hypothesis	352.039	9	39.115	.774	.640		
		Error	9801.480	194	50.523				

Appendix 14: Summary of ANOVA's of length specific growth rates of Chinook parr deprived of food for 10 or 16 weeks in winter (treatments) or fed twice weekly to satiation (control).

Dates of Sampling	**ANOVA**								**Post Hoc**	
	Source		**Sum of Squares**	**df**	**Mean Square**	**F**	**Prob.**	**Control vs.**	**Prob.**
11/19 – 1/28	Treatment	Hypothesis	.005	2	.002	8.137	.010	10 week	.092
		Error	.003	9	.000			16 week	.008
1/28 – 2/18	Treatment	Hypothesis	.003	2	.002	.391	.687	10 week	.663
		Error	.040	9	.004			16 week	.885
2/18 – 3/19	Treatment	Hypothesis	.003	2	.002	2.950	.103	10 week	.093
		Error	.005	9	.001			16 week	.692
3/19 – 4/8	Treatment	Hypothesis	.007	2	.003	2.833	.111	10 week	.950
		Error	.010	9	.001			16 week	.125
4/8 – 5/13	Treatment	Hypothesis	.001	2	.000	1.418	.291	10 week	.798
		Error	.003	9	.000			16 week	.268
5/13 – 5/27	Treatment	Hypothesis	.039	2	.019	.459	.646	10 week	.652
		Error	.378	9.005	.042			16 week	.850
	Tank(Treatment)	Hypothesis	.378	9	.042	3.444	.000		
		Error	7.461	611	.012				
5/27 – 6/10	Treatment	Hypothesis	.176	2	.088	14.873	.001	10 week	.175
		Error	.053	9.037	.006			16 week	.001
	Tank(Treatment)	Hypothesis	.053	9	.006	1.070	.383		
		Error	3.285	594	.006				
6/10 – 6/22	Treatment	Hypothesis	.038	2	.019	2.401	.131	10 week	.200
		Error	.100	12.486	.008			16 week	.792
	Tank(Treatment)	Hypothesis	.065	9	.007	.337	.962		
		Error	3.801	178	.021				

Appendix 14 continued: Summary of ANOVA's of length specific growth rates of Chinook parr deprived of food for 10 or 16 weeks in winter (treatments) or fed twice weekly to satiation (control).

Dates of Sampling	ANOVA							Post Hoc	
	Source		Sum of Squares	df	Mean Square	F	Prob.	Control vs.	Prob.
6/22 – 7/8	Treatment	Hypothesis	.023	2	.011	4.517	.033	10 week	.801
		Error	.033	12.925	.003			16 week	.030
	Tank(Treatment)	Hypothesis	.020	9	.002	.361	.952		
		Error	1.086	174	.006				
7/8 – 7/22	Treatment	Hypothesis	.097	2	.049	3.560	.070	10 week	.097
		Error	.129	9.501	.014			16 week	.129
	Tank(Treatment)	Hypothesis	.126	9	.014	2.045	.037		
		Error	1.212	177	.007				

Appendix 15: Summary of ANOVA's of weight specific growth rates of Chinook parr deprived of food for 10 or 16 weeks in winter (treatments) or fed twice weekly to satiation (control).

Dates of Sampling	ANOVA							Post Hoc	
	Source		**Sum of Squares**	**df**	**Mean Square**	**F**	**Prob.**	**Control vs.**	**Prob.**
11/19 – 1/28	Treatment	Hypothesis	.108	2	.054	36.026	.000	10 week	.000
		Error	.013	9	.001			16 week	.000
1/28 – 2/18	Treatment	Hypothesis	.335	2	.167	4.329	.048	10 week	.073
		Error	.348	9	.039			16 week	1.000
2/18 – 3/19	Treatment	Hypothesis	.095	2	.047	6.601	.017	10 week	.204
		Error	.065	9	.007			16 week	.234
3/19 – 4/8	Treatment	Hypothesis	.067	2	.033	1.578	.259	10 week	.975
		Error	.190	9	.021			16 week	.281
4/8 – 5/13	Treatment	Hypothesis	.019	2	.009	2.802	.113	10 week	.696
		Error	.030	9	.003			16 week	.102
5/13 – 5/27	Treatment	Hypothesis	7.060	2	3.530	9.583	.006	10 week	.436
		Error	3.317	9.003	.368			16 week	.006
	Tank(Treatment)	Hypothesis	3.317	9	.369	3.803	.000		
		Error	59.124	610	.097				
5/27 – 6/10	Treatment	Hypothesis	3.985	2	1.992	16.062	.001	10 week	.511
		Error	1.118	9.014	.124			16 week	.001
	Tank(Treatment)	Hypothesis	1.117	9	.124	1.323	.221		
		Error	57.104	609	.094				
6/10 – 6/22	Treatment	Hypothesis	.069	2	.035	.135	.876	10 week	.758
		Error	2.597	10.098	.257			16 week	.989
	Tank(Treatment)	Hypothesis	2.381	9	.265	1.514	.146		
		Error	31.470	180	.175				

Appendix 15 continued: Summary of ANOVA's of weight specific growth rates of Chinook parr deprived of food for 10 or 16 weeks in winter (treatments) or fed twice weekly to satiation (control).

Dates of Sampling	ANOVA							Post Hoc	
	Source		Sum of Squares	df	Mean Square	F	Prob.	Control vs.	Prob.
6/22 – 7/8	Treatment	Hypothesis	2.713	2	1.356	1.495	.268	10 week	.606
		Error	9.479	10.451	.907			16 week	.185
	Tank(Treatment)	Hypothesis	8.066	9	.896	.835	.585		
		Error	196.455	183	1.074				
7/8 – 7/22	Treatment	Hypothesis	118.616	2	59.308	1.055	.385	10 week	.909
		Error	534.634	9.514	56.192			16 week	.364
	Tank(Treatment)	Hypothesis	515.315	9	57.257	1.691	.094		
		Error	6364.237	188	33.852				

Appendix 16: Summary of ANOVA's of condition factor of Chinook parr deprived of food for 10 or 16 weeks in winter (treatments) or fed twice weekly to satiation (control).

Date of Sampling	ANOVA							Post Hoc	
	Source		**Sum of Squares**	**df**	**Mean Square**	**F**	**Prob.**	**Control vs.**	**Prob.**
11/19	Treatment	Hypothesis	.472	2	.236	24.023	.000	10 week	.083
		Error	.089	9.017	.010			16 week	.000
	Tank(Treatment)	Hypothesis	.088	9	.010	2.023	.036		
		Error	1.730	356	.005				
1/28	Treatment	Hypothesis	1.123	2	.562	113.400	.000	10 week	.000
		Error	.045	9.023	.005			16 week	.000
	Tank(Treatment)	Hypothesis	.045	9	.005	1.038	.409		
		Error	1.555	326	.005				
2/18	Treatment	Hypothesis	1.509	2	.755	122.339	.000	10 week	.080
		Error	.056	9.016	.006			16 week	.000
	Tank(Treatment)	Hypothesis	.056	9	.006	1.529	.136		
		Error	1.312	325	.004				
3/19	Treatment	Hypothesis	.799	2	.400	34.157	.000	10 week	.128
		Error	.105	9.004	.012			16 week	.000
	Tank(Treatment)	Hypothesis	.105	9	.012	2.931	.002		
		Error	1.342	336	.004				
4/8	Treatment	Hypothesis	1.364	2	.682	56.363	.000	10 week	.025
		Error	.109	9.002	.012			16 week	.000
	Tank(Treatment)	Hypothesis	.109	9	.012	2.474	.009		
		Error	3.591	734	.005				
5/13	Treatment	Hypothesis	.425	2	.212	11.597	.003	10 week	.278
		Error	.167	9.092	.018			16 week	.002
	Tank(Treatment)	Hypothesis	.167	9	.019	3.094	.001		
		Error	5.977	999	.006				

Appendix 16 continued: Summary of ANOVA's of condition factor of Chinook parr deprived of food for 10 or 16 weeks in winter (treatments) or fed twice weekly to satiation (control).

Date of Sampling	ANOVA							Post Hoc	
	Source		**Sum of Squares**	**df**	**Mean Square**	**F**	**Prob.**	**Control vs.**	**Prob.**
5/27	Treatment	Hypothesis	.073	2	.036	10.062	.005	10 week	.929
		Error	.033	9.016	.004			16 week	.008
	Tank(Treatment)	Hypothesis	.033	9	.004	.932	.496		
		Error	2.400	619	.004				
6/10	Treatment	Hypothesis	.015	2	.007	1.705	.235	10 week	.749
		Error	.038	9.029	.004			16 week	.253
	Tank(Treatment)	Hypothesis	.038	9	.004	1.165	.315		
		Error	2.195	601	.004				
6/22	Treatment	Hypothesis	3.99E-005	2	1.99E-005	.300	.747	10 week	.886
		Error	.001	10.239	6.65E-005			16 week	.616
	Tank(Treatment)	Hypothesis	.001	9	6.65E-005	.997	.444		
		Error	.012	178	6.67E-005				
7/8	Treatment	Hypothesis	.004	2	.002	1.098	.368	10 week	.586
		Error	.019	10.785	.002			16 week	.999
	Tank(Treatment)	Hypothesis	.016	9	.002	.590	.804		
		Error	.515	176	.003				
7/22	Treatment	Hypothesis	.002	2	.001	.650	.539	10 week	.430
		Error	.017	12.586	.001			16 week	.838
	Tank(Treatment)	Hypothesis	.011	9	.001	.331	.964		
		Error	.623	173	.004				

Appendix 17: Summary of ANOVA's of hematocrit of Chinook parr deprived of food for 10 or 16 weeks in winter (treatments) or fed twice weekly to satiation (control).

Date of Sampling	ANOVA							Post Hoc	
	Source		Sum of Squares	df	Mean Square	F	Prob.	Control vs.	Prob.
1/28	Treatment	Hypothesis	22.788	2	11.394	1.526	.269	10 week	.574
		Error	67.318	9.017	7.466			16 week	.779
	Tank(Treatment)	Hypothesis	67.201	9	7.467	1.118	.357		
		Error	708.122	106	6.680				
2/18	Treatment	Hypothesis	.150	2	.075	.377	.696	10 week	.926
		Error	1.797	9.005	.200			16 week	.719
	Tank(Treatment)	Hypothesis	1.798	9	.200	5.111	.000		
		Error	4.105	105	.039				
3/19	Treatment	Hypothesis	196879.044	2	98439.522	2.098	.178	10 week	.167
		Error	425552.337	9.072	46910.654			16 week	.643
	Tank(Treatment)	Hypothesis	423319.218	9	47035.469	1.673	.106		
		Error	2754848.232	98	28110.696				
4/8	Treatment	Hypothesis	.477	2	.239	1.949	.198	10 week	.209
		Error	1.107	9.040	.122			16 week	.790
	Tank(Treatment)	Hypothesis	1.107	9	.123	3.072	.003		
		Error	3.924	98	.040				
5/13	Treatment	Hypothesis	132.292	2	66.146	6.334	.019	10 week	.594
		Error	94.044	9.006	10.442			16 week	.017
	Tank(Treatment)	Hypothesis	94.003	9	10.445	1.684	.102		
		Error	663.556	107	6.201				
6/10	Treatment	Hypothesis	70.179	2	35.089	2.447	.106	10 week	.373
		Error	372.856	26	14.341			16 week	.093
7/8	Treatment	Hypothesis	206.726	2	103.363	7.751	.002	10 week	.012
		Error	346.722	26	13.335			16 week	.920

Appendix 18: Summary of ANOVA's of gill Na^{+}/K^{+} ATPase activity of Chinook parr deprived of food for 10 or 16 weeks in winter (treatments) or fed twice weekly to satiation (control).

Date of Sampling	ANOVA							Post Hoc	
	Source		Sum of Squares	df	Mean Square	F	Prob.	Control vs.	Prob.
1/28	Treatment	Hypothesis	.252	2	.126	1.714	.230	10 week	.339
		Error	.717	9.727	.074			16 week	.914
	Tank(Treatment)	Hypothesis	.654	9	.073	.636	.747		
		Error	1.256	11	.114				
2/18	Treatment	Hypothesis	.368	2	.184	5.089	.031	10 week	.816
		Error	.344	9.504	.036			16 week	.034
	Tank(Treatment)	Hypothesis	.328	9	.036	1.325	.332		
		Error	.275	10	.028				
3/19	Treatment	Hypothesis	.094	2	.047	.659	.539	10 week	.664
		Error	.679	9.492	.072			16 week	.444
	Tank(Treatment)	Hypothesis	.643	9	.071	.939	.530		
		Error	.836	11	.076				
4/8	Treatment	Hypothesis	.256	2	.128	1.189	.346	10 week	.382
		Error	1.031	9.593	.107			16 week	.959
	Tank(Treatment)	Hypothesis	.961	9	.107	.779	.640		
		Error	1.507	11	.137				
5/13	Treatment	Hypothesis	.959	2	.479	1.471	.278	10 week	.479
		Error	3.037	9.321	.326			16 week	.921
	Tank(Treatment)	Hypothesis	2.955	9	.328	1.438	.281		
		Error	2.511	11	.228				
6/10	Treatment	Hypothesis	.153	2	.076	.064	.938	10 week	.957
		Error	23.887	20	1.194			16 week	.940
7/8	Treatment	Hypothesis	.340	2	.170	1.124	.344	10 week	.959
		Error	3.173	21	.151			16 week	.383

Appendix 19: Summary of ANOVA's of whole-body lipid content of Chinook parr deprived of food for 10 or 16 weeks in winter (treatments) or fed twice weekly to satiation (control).

Date of Sampling	ANOVA							Post Hoc	
	Source		**Sum of Squares**	**df**	**Mean Square**	**F**	**Prob.**	**Control vs.**	**Prob.**
1/28	Treatment	Hypothesis	8.11E-005	1	8.11E-005	.122	.739		
		Error	.004	6	.001				
	Tank(Treatment)	Hypothesis	.004	6	.001	2.000	.179		
		Error	.003	8	.000				
2/18	Treatment	Hypothesis	.000	1	.000	.342	.580		
		Error	.003	6	.000				
	Tank(Treatment)	Hypothesis	.003	6	.000	2.017	.176		
		Error	.002	8	.000				
5/13	Treatment	Hypothesis	6.87E-005	2	3.43E-005	.060	.942	10 week	.936
		Error	.005	9	.001			16 week	.979
	Tank(Treatment)	Hypothesis	.005	9	.001	1.385	.293		
		Error	.005	12	.000				
7/22	Treatment	Hypothesis	.000	2	.000	1.882	.208	10 week	.216
		Error	.001	9	.000			16 week	.344
	Tank(Treatment)	Hypothesis	.001	9	.000	.453	.880		
		Error	.003	12	.000				

Appendix 20: Summary of ANOVA's of protein content of Chinook parr deprived of food for 10 or 16 weeks in winter (treatments) or fed twice weekly to satiation (control).

Date of Sampling	ANOVA							Post Hoc	
	Source		Sum of Squares	df	Mean Square	F	Prob.	Control vs.	Prob.
1/28	Treatment	Hypothesis	.004	1	.004	.007	.935		
		Error	3.182	6	.530				
	Tank(Treatment)	Hypothesis	3.182	6	.530	3.501	.053		
		Error	1.212	8	.151				
2/18	Treatment	Hypothesis	4.546	1	4.546	10.878	.016		
		Error	2.508	6	.418				
	Tank(Treatment)	Hypothesis	2.508	6	.418	1.420	.315		
		Error	2.355	8	.294				
5/13	Treatment	Hypothesis	2.867	2	1.433	6.169	.021	10 week	.621
		Error	2.091	9	.232			16 week	.019
	Tank(Treatment)	Hypothesis	2.091	9	.232	.926	.536		
		Error	3.010	12	.251				
7/22	Treatment	Hypothesis	.476	2	.238	3.912	.049	10 week	.995
		Error	.734	12.073	.061			16 week	.071
	Tank(Treatment)	Hypothesis	.484	9	.054	.213	.985		
		Error	2.523	10	.252				

Appendix 21: Summary of ANOVA's of moisture content of Chinook parr deprived of food for 10 or 16 weeks in winter (treatments) or fed twice weekly to satiation (control).

Date of Sampling	ANOVA							Post Hoc	
	Source		Sum of Squares	df	Mean Square	F	Prob.	Control vs.	Prob.
1/28	Treatment	Hypothesis	1.525	1	1.525	.340	.581		
		Error	26.939	6	4.490				
	Tank(Treatment)	Hypothesis	26.939	6	4.490	1.802	.216		
		Error	19.934	8	2.492				
2/18	Treatment	Hypothesis	12.763	1	12.763	4.344	.082		
		Error	17.627	6	2.938				
	Tank(Treatment)	Hypothesis	17.627	6	2.938	3.291	.062		
		Error	7.141	8	.893				
5/13	Treatment	Hypothesis	6.027	2	3.014	2.557	.132	10 week	.649
		Error	10.606	9	1.178			16 week	.116
	Tank(Treatment)	Hypothesis	10.606	9	1.178	.686	.710		
		Error	20.623	12	1.719				
7/22	Treatment	Hypothesis	.738	2	.369	.370	.701	10 week	.727
		Error	8.962	9	.996			16 week	.762
	Tank(Treatment)	Hypothesis	8.962	9	.996	1.201	.375		
		Error	9.949	12	.829				

Appendix 22: Summary of ANOVA's of ash content of Chinook parr deprived of food for 10 or 16 weeks in winter (treatments) or fed twice weekly to satiation (control).

Date of Sampling	ANOVA							Post Hoc	
	Source		**Sum of Squares**	**df**	**Mean Square**	**F**	**Prob.**	**Control vs.**	**Prob.**
1/28	Treatment	Hypothesis	.044	1	.044	1.674	.243		
		Error	.157	6	.026				
	Tank(Treatment)	Hypothesis	.157	6	.026	5.479	.016		
		Error	.038	8	.005				
2/18	Treatment	Hypothesis	.163	1	.163	19.663	.004		
		Error	.050	6	.008				
	Tank(Treatment)	Hypothesis	.050	6	.008	.294	.923		
		Error	.226	8	.028				
5/13	Treatment	Hypothesis	.025	2	.013	1.054	.388	10 week	.441
		Error	.108	9	.012			16 week	.464
	Tank(Treatment)	Hypothesis	.108	9	.012	.700	.699		
		Error	.206	12	.017				
7/22	Treatment	Hypothesis	.003	2	.001	.235	.796	10 week	.922
		Error	.051	8.275	.006			16 week	.974
	Tank(Treatment)	Hypothesis	.049	8	.006	.943	.524		
		Error	.065	10	.006				